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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

154th Session (1941–42) Part 3

CONTENTS

Page

Proceedings, 18 June 1942 217

Fasciated *Ranunculus bulbosus* from St. Annes-on-Sea, Lancs. [Exhibit.] By Sir Cuthbert C. Grundy 217

Proceedings, 9 July 1942 218

On a method of preparing large sections of plants by grinding. [Title only.] By K. N. Kaul 218

A symposium on Intertidal Zonation of animals and plants ... 219

(1) The causes of the vertical and horizontal distribution of organisms between tidemarks in South Africa. By T. A. Stephenson 219

(2) Some intertidal enigmas. By John Colman 232

(3) The significance of the exposure factor in relation to zonation. By E. Marion Delf 234

(4) Zonation of Marine Algae on the sea-shore. By V. J. Chapman 239

The Entomostraca of the bottom deposits of Windermere. By D. J. Scourfield 253

Aquilegia Einseleana Schultz forma Schleicheri forma nova. By M. Skalińska 259

[*For continuation of Contents see back page.*]

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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

154th Session (1941–2) Part 3

PROCEEDINGS OF THE GENERAL MEETING
18 June 1942

Dr. E. S. Russell, O.B.E., M.A., President,
in the Chair.

The Proceedings of the Anniversary Meeting held on Thursday, 28 May 1942, having been circulated, were taken as read and confirmed.

The President announced that Prof. F. E. Weiss had made a donation to the Library, and Dr. Catherine A. Raisin one of £5 towards the cost of preserving during the War some of the Society's treasures. A vote of thanks was accorded for these generous gifts.

Read for the first time certificates of recommendation of the following candidates for Fellowship: in favour of James Maxwell McConnell Fisher, M.A., and Charles Aubrey Hamilton Franklyn, M.D.

Exhibited, on behalf of Sir Cuthbert C. Grundy, F.L.S., a photograph of a fasciated *Ranunculus bulbosus* from St. Annes-on-Sea, Lancashire. *Characters.*—A flattened axis 1 cm. broad, with (i) several normal flowering lateral branches at mid-height, arranged somewhat spirally; (ii) a second group of branches higher up, small and not flowering, and also more or less spirally arranged; (iii) a third group of small branches; and (iv) a dense bunch of flowers in the form of a terminal capitulum. The Botanical Secretary pointed out that we know little of the causes of such fasciation, but that when the causes have been established their geographic distribution will become interesting, and, therefore, their record is not superfluous.

The symposium on Intertidal zonation of animals and plants was opened by Prof. T. A. Stephenson with an address entitled 'The causes of the vertical and horizontal distribution of organisms between tide marks in South Africa'. He was followed by Dr. J. Colman on 'Some intertidal enigmas,' and Dr. E. M. Delf, F.L.S., on 'The significance of the exposure factor in relation to zonation'.

The paper promised by Dr. V. J. Chapman was postponed, the author being unavoidably absent. The subjects raised in the papers were discussed by those who had already spoken and by Dr. G. P. Bidder and Prof. L. Newton. [The symposium is printed in full, p. 219.]

PROCEEDINGS OF THE GENERAL MEETING
9 July 1942

Dr. E. S. Russell, O.B.E., M.A., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 18 June 1942, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—Dr. A. S. Corbet, Prof. James Small, and The Royal College of Surgeons of England.

Read for the second time certificates of recommendation of the following candidates for Fellowship : in favour of James Maxwell McConnell Fisher, M.A., and Charles Aubrey Hamilton Franklyn, M.D.

The following candidate, whose name was read for the third time, was balloted for and elected a Fellow : Peter John Bell.

The President reported the deaths of the following members : Mr. C. C. A. Monro, F.L.S., and Dr. C. Davies Sherborn, A.L.S.

In a continuation of the Discussion on ' Intertidal zonation of animals and plants ', Mr. A. D. Cotton gave an account of Dr. V. J. Chapman's communication, ' Zonation of marine algae on the sea-shore '.

The following communications were read and discussed :—

Mr. D. J. Scourfield. The Entomostraca of the bottom deposits of Windermere. (Discussed by Prof. F. E. Weiss ; Mr. Scourfield replied.) [Printed in full, p. 253.]

Mr. K. N. Kaul. On a method of preparing large sections of plants by grinding. (Discussed by the President and Dr. C. R. Metcalfe.) A description of the method may be found in ' Current Science,' iv, p. 99, for August, 1935.

Dr. Maria Skalińska. *Aquilegia Einseleana* Schultz, forma *Schleicheri*, forma nova. (Communicated by Dr. T. A. Sprague.) (Discussed by Dr. T. A. Sprague.) [Printed in full, p. 259.]

The following paper was read in title,—

' A revision of the Indian and Burmese species of *Sageraea*.' By Dr. Debabrata Chatterjee. [Printed in full, p. 263.]

The President then declared the Session of 1941–2 closed.

A SYMPOSIUM ON INTERTIDAL ZONATION OF ANIMALS AND PLANTS.

(1) THE CAUSES OF THE VERTICAL AND HORIZONTAL DISTRIBUTION OF ORGANISMS BETWEEN TIDEMARKS IN SOUTH AFRICA.

By T. A. Stephenson.

When Dr. Russell suggested that I might open a discussion on the subject of zonation at a meeting of the Linnean Society, it so happened that I had already written the first draft of a paper which attempts to elucidate the reasons for both the vertical zonation and the horizontal distribution round the coast of the common South African intertidal organisms, and which is based upon information collected by my collaborators and myself during the past ten years *. This paper will not be ready for publication for some time, but an exchange of views on some of the ideas contained in it will undoubtedly be of value to me personally, and I hope may also be of interest to the Society. The following summary represents, however, nothing more than an abbreviated preliminary review of the situation, and is therefore provisional. The South African coast, passing as it does from subtropical conditions in the east to almost subantarctic conditions in the west, probably presents information which is as likely to contribute usefully to the problem of zonation as a whole as any that could be found. Up to the present it has not been attempted, in more than a preliminary manner, to correlate this information with accounts of zonation in other parts of the world ; but such a correlation is projected. In referring to the literature of zonation I should like to say that it is particularly pleasing that Dr. J. S. Colman is able to take part in today's discussion, because his paper in the ' Journal of the Marine Biological Association ' for 1933 on the nature of intertidal zonation marks a new starting point for the study of zonation in this country, and it would therefore have been decidedly lamentable if Dr. Colman had been unable to attend this meeting.

The formal proof that the zonation observed on the shore is due to the interaction of a stated set of factors can only be obtained experimentally. It is important to remember, however, that what is visible on the shore is itself the result of a large-scale natural experiment : the experiment of exposing to an intertidal environment the thousands of eggs, spores and larvae flung against the rocks by the sea. Contributions to the solution of the problem of zonation may therefore be expected from an interpretation of the facts observed on the shore (i.e. of the result of the natural experiment), as well as from an interpretation of the results of laboratory

* Detailed information connected with the ecology of the South African coast will be found in papers in Trans. Roy. Soc. S. Africa, xxiv, p. 341 ; xxvi, pp. 49, 67 ; xxviii, pp. 255, 331 ; in Ann. Natal Mus. ix, pp. 1, 21, 47, 83, 113, 283, 345 ; in Journ. Linn. Soc. Lond., Zool. xl, p. 487 ; in Proc. Linn. Soc. Lond. Session 148, p. 74; in Journ. Exper. Biol. xi, p. 162 ; and in a summary privately printed by the author (1941).

experiments. While the interpretation of the latter is likely to be easier than that of the former, because such experiments are small in scale and can deal with one variable at a time, the field observations have the advantage that they record the results of experiments on a sweeping scale unattainable in the laboratory. These results ensue from combinations of conditions which do in fact occur on the shore, whereas laboratory experiments inevitably take place in a somewhat abnormal environment, and cannot simulate natural conditions beyond a certain point. Supplementary information may of course be gained by deliberate experimental interference with the life of the shore by human agencies ; but here again the scale can never be as extensive as that of the interaction of natural forces on a whole coastline.

In the following discussion single factors will be treated separately as far as possible, but since the distribution of any organism between tidemarks tends to be due to several factors working together rather than to a single isolated cause, it is doubtful whether much is to be gained by too great an insistence on the part played by each factor in a complex. In other words, if it seems clear that the upper limit of a species is determined by the degree of its ability to resist desiccation, acting together with its responses to temperature and light, we at least know something definite about that species even if we have not yet been able to disentangle the effects due to each of the interacting variables.

NATURE OF SUBSTRATUM.—The present discussion is limited to the fauna and flora of rocky areas.

Composition of the rock.—The intertidal rocks around South Africa include granite, hard quartzitic sandstones, soft calcareous sandstones (sandgrains in a calcareous cement), dolerite, conglomerates, slate-like rocks, marble and other formations. Although the nature of the rock may exert a certain selective influence on the organisms which attempt to colonize it (for instance, most of the types of rock are not susceptible to boring organisms, whereas the calcareous sandstone is susceptible), and although minor variations in zonation may be attributed to it, nevertheless the main outlines of zonation, and the orderly march of the horizontal distribution of species along the major stretches of coast, seem to be quite unaffected by it. Thus, where granite and hard sandstone occur intermingled on the same beach, the zonation is essentially the same on both ; and may be the same again on slate-like rocks at no great distance away. At one locality where outcrops of granite and marble occurred close to each other, there appeared to be no marked zonational differences between the two. The arrangement of organisms on areas of calcareous sandstone often shows divergences from the normal which at first sight seem to be connected with the composition of the rock, but which on closer examination prove, almost certainly, to be due to other causes.

Configuration of the rock.—Texture of the rock-surface is one consequence of its composition which, again, seems to exert only minor effects on zonation. *The configuration of the major rocky masses*, however, consequent upon the way in which each type of rock tends to weather, has certain definite effects. Thus granite tends to weather into smooth slopes and rounded boulders, hard sandstone into ledges and rectangular

shapes, slate and shale into jagged ridges, and so on. These varying shapes are effective in one sense in that they may present the zones in a diagrammatic form (as on smooth slopes) or break them up into a kaleidoscopic series of fragments (as on a tumbled chaos of rocks) ; but they are also effective in their interactions with other factors. Thus the shapes and arrangement of the rocks interact with the waves and help to determine the type and degree of wave-action to which any particular group of organisms is exposed. This in its turn causes modifications in the zonation. The responses of organisms to variations in wave-action are so important that they will be dealt with separately below. Meanwhile other local effects due to the shape of the rocks may be noted, such as the distribution of caves, overhangs and other shaded surfaces which introduce variations in light-intensity. Shade, however, tends to encourage the cryptofauna and flora and to restrict the species tolerant of sunshine. Its action thus splits the biota into two sections, in *each* of which zonation is evident ; the existence of shade provides a distinct habitat rather than elucidating the problem of zonation on sunny slopes.

A particularly neat example of the inability of rock-formation to affect the broad *horizontal* distribution of species is provided by the intertidal rocks at Isipingo in Natal, and at Bats Cave Rocks, near East London (see Ann. Natal Mus. IX, pp. 24, 97, 104). At each of these localities, which are some 300 miles apart, the rock is calcareous sandstone in the form of two platforms, one above the other, both with cliffed edges, the lower platform being intertidal and with broken rocks at its foot. The soft rock of the platforms is much pitted and presents a peculiar series of pools, potholes and terraces. Here, if anywhere, given a formation so extraordinary, parallel effects should be produced, but although the *zonation* is modified as compared with that of an even slope *, there is little, if any, effect on the composition of the fauna and flora as a whole. The biota of Isipingo is that of Natal, with local adaptations ; that of Bats Cave rocks is a population typical of the geographical region in which it occurs (i.e., is similar to that of the south coast), and lacks the distinctive features of the Natal biota. At both localities the queer rock-formation has therefore encouraged local variations, but they are variations from the norm *for that part of the coast*, and not similar total populations, in different districts, established as a result of the existence of a particular rock-formation. It is the difference in mean annual surface-temperature which is the decisive factor here, the similar rock-formation being peculiarly ineffective.

The proximity of sand.—There is little doubt that the proximity of any considerable body of sand to a rocky area affects the population of the adjacent rock. On the west coast there is a tendency for the replacement of the Cochlear mosaic in such areas by other communities, such as beds of *Mytilus* and sea anemones (*Bunodactis reynaudi*). The occurrence of *Mytilus meridionalis*, moreover, seems to be favoured by the proximity of sand (and beds of this mussel may even occur on a sandy foundation),

* By the introduction of peculiarities of wave-action, of an unusual relationship between sunny and shaded areas and between vertical and horizontal faces, and other complications.

that of *M. crenatus* being inhibited by it. Since, however, proximity of sand and a certain degree of reduction in wave-action often go together, the effects of the two are not easily disentangled.

The width of the rocky tract may affect distribution in that organisms which tend to occupy its whole width where it is narrow sometimes die out to landward where it is wide. Thus at certain localities barnacles are absent or reduced on inshore rocks at levels which they colonize freely to seaward.

Desiccation.—There appears to be no doubt that degree of ability to withstand desiccation is one of the vital factors operative between tide-marks. It may affect organisms in two ways : (*a*) by extreme action over short periods, and (*b*) by repeated action over long ones. Such action is *intensified* by increased temperature and air-movement, and possibly *supplemented* by light-effects, in varying degrees under different circumstances ; and *mitigated* by certain other agencies.

Extreme action over a short period.—This is seen occasionally when a hot, dry wind persists for two or three consecutive days, in summer, coinciding with spring tides. This can result in the death of thousands of fronds or whole plants of certain algae of the lower levels (e.g. *Hypnea spicifera*, *Gigartina radula* and *G. stiriata*), while species characteristic of higher levels, such as *Chaetangium ornatum*, may be quite unharmed. Here the fatalities appear to be due to the combined action of desiccation, heat and light, but as the light is presumably not abnormally intense on such occasions, it could be effective only if the action of heat and drying rendered the tissues of the plants more susceptible than normally to its action. It seems to be a fair conclusion that *Chaetangium ornatum* can establish itself higher up than the other species mentioned because of its greater resistance to these agencies. It is easy to imagine that occurrences less drastic than those just described might destroy many animal larvae and young plants.

Repeated action over long periods.—The controlling effects of desiccation are probably ordinarily exerted by means of repeated exposure to its action, such exposure varying in length and frequency at different levels and sometimes covering several days at a time. That intertidal organisms do possess, in varying degrees, the ability to withstand prolonged desiccation is certain, both from field observations and experiments. Thus, to take only one example from among many, one observes, widespread over the Indo-Pacific tropics, millions of oysters (*Ostrea cucullata*) inhabiting levels on the intertidal rocks where they are baked in the sun for a high proportion of their lives and experience body-temperatures such as 45° C. and more. It can hardly be doubted that these oysters live where they do because they are resistant to high temperatures and protected against desiccation, though the reason why they do not extend to *lower* levels is to be sought elsewhere. Equally clearly species without such powers cannot extend to high levels. From the experimental side it is well known that certain snails and barnacles of the higher levels can be dried for long periods and will yet survive ; and that species from different levels may show graded reactions to desiccation. A particularly neat example of this has been provided by Broekhuysen (Trans. Roy. Soc. S. Africa, xxviii, p. 255), who showed that a series of South African inter-

tidal gastropods inhabiting different levels showed a graded ability to withstand desiccation, which corresponds extraordinarily well in the main with the order of their occurrence on the shore.

Interaction of desiccation with other factors.—Both high temperatures and wind will increase the rate of desiccation and augment its total amount within a given period. That the drying action of these agencies is of more importance than the actual temperature involved (at least in some cases and in some latitudes), is suggested by experiments such as those of Broekhuysen already mentioned. Thus Broekhuysen found that adult snails showed a graded resistance to desiccation even when *unaccompanied by any unduly high temperature* ; and that, in addition, although they showed a graded resistance to high temperatures unaccompanied by desiccation, their lethal temperatures (when submerged) lay at a higher level than anything they were likely to experience (at any rate frequently) in their natural habitats, and, therefore, hardly seemed likely to be acting as primary limiting factors in their vertical distribution. His experiments also suggest, however, that high temperatures may reduce the resistance of the snails to desiccation, and might thus become of greater importance in the tropics. As Broekhuysen has pointed out, furthermore, the temperatures lethal to the young of the molluscs which he studied have not been determined, and these may be lower than those lethal to the adults. The relationship between temperature and desiccation on the one hand and *light* on the other also needs further study. Organisms high up on the shore are presumably exposed to the same light-intensities as those lower down (while exposed to the air), and it is possible, as has already been noted, that the action of drying and heating may, after a certain point, render them susceptible to light-intensities which normally have no harmful effects on them.

Factors which mitigate desiccation.—Sun and wind are important in South Africa because not only is it a windy country, but the proportion of sunny days is high, the sun is powerful in summer, and even in winter its effects are by no means negligible. The higher intertidal rocks therefore do frequently become very dry and hot. These conditions are of course more accentuated in summer than in winter, and are mitigated by rain (though on some parts of the coast the major rainfall is concentrated in a particular season of the year), but they are more regularly mitigated in certain regions by other features. Thus the South African coast as a whole is open and oceanic in nature, and wave-action is normally strong enough to keep the seaward edge of the intertidal zone wet during low water ; and although the time of low water of springs varies on different parts of the coast, it always occurs in the morning and frequently before the maximum power of the sun has been reached. On the west coast, furthermore, a morning mist is of sufficiently frequent occurrence to have a significant effect on intertidal life.

The sharpness of certain upper limits.—While some organisms die out gradually over a fairly wide upper limit, others disappear with remarkable suddenness. The behaviour of lithothamnia * in South Africa is signifi-

* ' Lithothamnia ' : used here as a general term covering encrusting Corallinaceae of the genera *Lithothamnion*, *Melobesia*, etc.

cant in this connection, and is seen particularly clearly on the west coast. The relevant points are as follows: (i) The bulk of the lithothamnial growth tends to clothe the lower, wetter rocks as a continuous carpet; and this growth has a remarkably sharp upper limit; (ii) the level of this upper limit varies in a most sensitive manner in correlation with the exact degree of wave-action to which any particular rocky face is habitually exposed: the wetter the place the higher the limit (up to a certain point); (iii) above the limit of the main growth the lithothamnia have a discontinuous distribution, reappearing locally (up to a certain level) wherever conditions are damper than normal, as in pools, crevices, shaded areas, and so on; (iv) occasionally, during some spell of favourable weather, thousands of minute plants of lithothamnia germinate on open rocks above the upper limit of the main growth of these organisms; but these perish as soon as the climatic pendulum swings against them. These facts suggest that lithothamnia can withstand a certain (often wide) range of exposure to desiccation and warming, but that the threshold beyond which these factors become lethal appears suddenly; the organisms extend their distribution as close as they possibly can towards the limits lethal to them, but cannot withstand repeated exposures of supra-liminal intensity. This will apply to many organisms other than lithothamnia.

Temperature.—Here the effects of air-temperature and water-temperature must be clearly distinguished, although they are interdependent.

Air-temperature.—This never becomes low enough in South Africa to cause inconvenience to intertidal organisms. It becomes high in varying degrees on all parts of the coast in summer, so that, as already mentioned, rock-surfaces exposed to direct sunshine commonly become markedly heated up, and the higher up an organism lives the less is this effect mitigated by the cooling action of waves and splash. Since, however, high air-temperatures and desiccation commonly act upon the organism at the same time and in the same sense, the temperature reinforcing the drying effect, nothing will be added on this head to what has been noted above when considering desiccation.

Water-temperature.—Here a distinction must be drawn between the temperature of the water in pools and that of the sea itself.

The temperature of rock-pools depends upon that of the sea at the time when the pools begin to be isolated, upon the weather on any particular day, and upon the exact specification of each pool (its level, size, depth, exposure to sunshine, etc.). Thus while, on the whole, pools high up the shore become warmer and remain warm for longer than those lower down, large pools and shaded pools will remain cooler, level for level, than small and sunlit ones. In South Africa it is also very evident that the population of pools exhibits a regular zonation which, though not the same as that on emerged surfaces, is parallel to it. This zonation must be due to some cause, and since desiccation in this case is eliminated, temperature and salinity take the centre of the stage. It has already been concluded that, for emerged animals, temperature-effects are probably subsidiary, though accessory to drying-effects; so that it may seem illogical to urge that in pools (in which, in South African temperate latitudes, lethal temperatures for snails seem rarely, if ever, to be reached) they are probably the leading factor, often acting together with variations

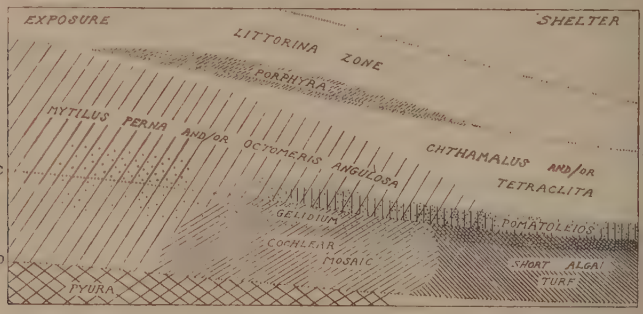
in salinity. It may, however, be remembered that animals and plants may find *optimum* conditions at temperatures and salinities well below their actual lethal limits: and the distribution observed in rock-pools does undoubtedly convey the impression that temperature variations are important in this habitat.

The temperature of the sea itself.—As the tide rises and falls, the warmth of the water affects all levels alike, and there is no suggestion that it has any effect on zonation. On the horizontal distribution of species round the South African coast, however, there seems to be no doubt that it has more effect than any other agent. The orderly change which takes place along the great stretches of coast, from the subtropical population of Natal to the very different cold-water population of the west coast, coincides so clearly in its major progress with the arrangement of oceanic currents round the southern end of the continent and with the east-to-west change in mean annual surface temperature, that it can hardly be doubted that the two series of changes are connected. There are, moreover, no other broad changes to which one can point which seem to be of sufficient amplitude to compete with those of temperature as primary controllers of the horizontal distribution of species, unless there is a significant difference between the amount of nutritive salts available for algae on the west coast and that available elsewhere. It is more probable that there is a particularly good supply available in the west, connected with the upwelling of cold inshore water, than that there is any actual deficiency farther east, since although the algal growth in the west is particularly exuberant, it is by no means scanty elsewhere.

Wave-action.—In the varying degrees of wave-action to which intertidal organisms may be exposed we have a controlling factor second to none in importance, and it is a factor which may be studied particularly favourably in South Africa, whose coasts are so widely open to oceanic waves and swells that maximal wave-action can attack them. At the same time the detail of the rock-formations is such as to provide an infinite series of gradations in shelter from waves, so that all degrees of shelter from, and exposure to, wave-action may be observed. Nothing is more obvious than the reaction of organisms to these gradations.

A specific example will probably clarify this statement better than anything else, and is provided by the population of the south coast of the Union as represented, for instance, at Port Elizabeth and Storms River (see the annexed figure). The arrangement of zones found on this coast in places subject to strong (but not maximal) wave-action will be considered as the norm, and departures from it as variations. A typical normal zonation shows a dense concentration of ascidians (*Pyura stolonifera*) below: then a well-developed mosaic of *Patella cochlear* with lithothamnion; above this a strong concentration of barnacles (especially *Octomeris angulosa*) and mussels (*Mytilus perna*): these thin out above and give place to the Littorina zone. There are variants of this scheme which may occur irrespective of any change in wave-action, but these do not concern us here. If we follow the changes which take place, however, as one proceeds from regions of strong or moderate to those of maximal wave-action, it is found that the Cochlear mosaic wanes and disappears, its place being taken by ascidians from below and *Mytilus* and *Octomeris*

from above, so that there is no longer any Cochlear zone. On the other hand, if we follow the zonation from its normal condition into more sheltered places we find that the Cochlear mosaic again disappears *, to be replaced this time, most commonly, by a moss-like turf of short algae: in this case the zone retains its identity, but the population changes. Other reactions which complicate the effect are as follows. *Octomeris* and *Mytilus* are seaward creatures and wane with more than a certain degree of shelter; whereas other important zone-indicators, the polychaet *Pomatoleios crosslandi* and the red alga *Gelidium pristoides*, disappear or become reduced in amount as wave-action increases, flourishing strongly with increased shelter. These facts may be interpreted as follows: *Patella cochlear* cannot maintain itself in quantity where wave-action is terrific, though it can stand a good deal. Where it cannot get a footing, *Octomeris*, *Mytilus* and *Pyura*, which appear to be able to withstand almost infinite battering, take its place. Where *P. cochlear* is present



A diagram illustrating the effect on zonation of exposure to different degrees of wave-action on the southern coast of South Africa. Only a selection of the organisms which may actually be present on the south coast is included here. The dotted lines A, B, C, and D represent the upper limits of the Littorina, Balanoid and Cochlear zones and of the sublittoral fringe. These lines descend from left to right because the zones become narrower as shelter from wave-action increases; maximal exposure to wave-action being represented on the left of the diagram, maximal shelter from it on the right, and average exposure about the centre. The diagram attempts to show how the organisms included in it are distributed over the several zones in relation to the different intensities of wave-action habitually experienced by them in different parts of the beaches.

in normal quantities, *Octomeris* and *Mytilus* are inhibited at the levels which it inhabits, because the continual browsing of the close-set limpets prevents the effective settling of their larvae, and they are therefore found primarily at levels too high for *P. cochlear*. In the sheltered places, again, there is too little water-movement for *P. cochlear*, and this time conditions are more favourable for short algae, *Pomatoleios* and *Gelidium*

* In former publications we have described the Cochlear mosaic as characteristic of situations exposed to strong wave-action, and waning with increased shelter. That it wanes also under *maximal* wave-action is a more recent discovery: at the time of writing our earlier papers, only submaximal wave-action had been seen.

pristoides, than for *Octomeris* and *Mytilus*, and these accordingly occupy much of the space available. Although this example refers to parts of the south coast, parallel reactions are universally visible on the east and west coasts also.

Mode of action of water disturbance.—That variations of the type just enumerated do in fact depend on local variations in wave-action can hardly be doubted, since there is no other major factor which fluctuates in the same way as do the communities mentioned. In what manner, however, is the wave-action effective? Clearly where wave-action is strong the organisms subjected to it are kept perpetually wet and cool even at low water, and are rarely, if ever, in danger from desiccation, excessive heat or excessive light; while in a sheltered place the reduction of wave-movement may expose them to all these things. There seem, however, to be other effects. Where wave-action is maximal, its power must be seen and heard to be believed; it might be supposed that no living thing could survive its impact. This is far from being the case. Although wave-swept rocks whose surface is relatively bare are sometimes seen, their bareness is more likely to be due to some particular variety of wave-action than to its actual force and weight; and on the whole areas subjected to maximal wave-action are densely populated. Although, as we have seen, species such as *Patella cochlear* seem unable to make a success there, presumably because of the strength of the mechanical impact, other species can not only withstand this, but flourish so exceedingly under it that the impression is conveyed that the turmoil of the waves is not only *not harmful* to them but is in itself beneficial. That perpetual wet and cool are not the only factors involved in the case of *Octomeris* and *Mytilus* is demonstrated by the fact that these species do well not only where they are more or less perpetually drowned by waves, but also in positions where they are exposed to the sun and wind for considerable periods, provided those periods are not too long. For *Patella cochlear*, too little wave-action as well as too much is evidently inimical; here, although increased exposure to the desiccation-heat-light complex, rather than reduced wave-movement in itself, may be decisive, it is not impossible that the latter may be a contributing factor.

Feeding habits.—During the course of the South African survey it was noted repeatedly that the small carnivorous whelk *Thais dubia*, which extends along the coast at least from Pondoland in the east to Port Nolloth in the west, is distributed in a curious way between tide-marks. While a limited number of individuals (often rather small ones) may usually be found at high levels where desiccation is strong, yet the bulk of the population occurs lower down, or at least in more seaward positions, commonly among barnacles. Broekhuysen appears to have found the key to this situation in his study of intertidal snails in the Cape Town district. He finds that *Thais dubia* is second only to *Littorina knysnaënsis* in its powers of resisting desiccation, and therefore *can* live at high levels; but also that its principal food-supply (certain barnacles and young limpets) is most abundant lower down; hence, apparently, the concentration of the snail at these levels. There seems to be little doubt that another effect connected with feeding-habits is produced by *Patella cochlear*. Where this limpet is abundant it occurs in such numbers

that its browsing-habits (connected with which there is experimental evidence as yet unpublished) have an inhibiting effect on the settlement and growth of other organisms. One result of this already noted appears to be the tendency, where *P. cochlear*, *Octomeris* and *Mytilus* occur abundantly together, for the bulk of the two latter to occupy a zone *above* the mosaic of the former—that is, above the levels which the limpet can colonize. Probably examples of this sort could be multiplied, and while many features of intertidal zonation evidently depend on other factors, the feeding-habits of some of the species concerned have their own definite effect at certain points in the whole pattern.

Competition for food and space.—At the upper levels there is a great deal of bare rock, or rock coated with sub-microscopic algae and lichens in a thin layer. At these levels there is clearly no lack of actual standing-room. The leading animals are limpets and snails which browse on the organic film over the rock, and outlying barnacles. The latter obtain planktonic food and are thus not in competition for food with the limpets and snails. The existence of bare areas at high levels may therefore be explained as the result of (*a*) limitation of the number of species able to colonize these areas for reasons connected with the desiccation complex, (*b*) the fact that even in a species resistant to desiccation some individuals appear to be more resistant than others, and (*c*) limitation of the food-supply : if the whole space available were occupied by snails and limpets there would probably be insufficient food to support them.

At the lower levels there is also competition for food, but also more of it. Here, however, bare rock becomes much less common and the density of organisms often very high. The problem of obtaining and keeping standing-room now becomes acute, so that many organisms never become seated on the rock at all, but upon and between each other. Under these conditions competition for space is undoubtedly a reality, and some organisms compete so successfully that they either exclude everything else over the area which they occupy, or at least dominate the area markedly so that they occupy the major part of the available space. A new feature is thus introduced into the population of such places, which may now be subdivided into (*a*) dominant forms and (*b*) epizoic (or epiphytic) and interstitial forms.

Salinity.—*Salinity of the open sea.*—We have no evidence that such variations in salinity as occur round the open coast have any important effect on the horizontal distribution of organisms. It is, moreover, rather remarkable how little local effect the outflow of rivers seems to have on the intertidal population. Conditions inside estuaries and lagoons are naturally modified as compared with the open coast, but the permanent effect extends surprisingly little, as a rule, beyond the actual river mouth, despite the fact that the temporary results of floods sometimes extend a long way beyond the river.

Rainfall.—The annual rainfall is very different in amount on the several parts of the South African coast, and is also differently distributed over the year. In some regions rain may often be heavy and persistent during the period of low water. Such rainfall may create a film of fresh water over the rocks, washing away temporarily much of the salt. This may

restrict the feeding activities of some animals for the time being, but we have no evidence that it produces any controlling effect on zonation on the open rock.

Rock-pools.—Here, if anywhere, variations in salinity should affect zonation. In pools situated at the lower levels there is hardly time, while they are isolated from the sea, for either a marked lowering of salinity due to rain or raising of it due to evaporation, except where pools are small : and even then the effect is of short duration and rectified as soon as the sea returns. At the higher levels there is more scope for change, and occasionally small pools dry out completely and leave crusts of salt. There is no doubt that the population of the higher pools in general is much poorer in species than that of the lower ones. There is also no doubt that the salinity in such pools varies within wide limits, since Broekhuysen (1940) has demonstrated a range of 1·28 Cl/L in high-level pools where the value in Cl/L for the sea was about 19·9. His experiments also showed that although the snails studied by him showed graded reactions to changes in salinity, such changes seemed unlikely on the whole to be acting as limiting factors in the distribution of adults on the shore. One of his snails, however, *Oxystele tigrina*, showed high resistance to salinity coupled with low resistance to desiccation ; this snail therefore keeps for the most part to pools, but can inhabit pools at moderately high levels where salinity-changes may be appreciable, being excelled in this respect only by *Littorina knysnaënsis*. Change in salinity can apparently be lethal to a snail in the following manner : it may at first induce more active crawling, but afterwards, if the snail has not escaped from the changing water, will cause cessation of crawling ; then, if the abnormal salinity is continued for long enough, the snail may die. It should also be noted, however, that in Broekhuysen's experiments the salinity actually demonstrated in the habitats of the snail was never as high as the salinity at which crawling ceased under experimental conditions, though it was sometimes *low* enough to cause cessation of crawling. Broekhuysen has also shown that temperature can affect the susceptibility of organisms to changes in salinity, and it is by no means impossible that an unfavourable combination of these factors may affect the sensitivity of the creature to intense light. Effects of salinity and temperature naturally become most urgent in pools whose water is not changed at high water of neap tides (or even, sometimes, at high water of springs). It will at least be reasonable to conclude that in rock-pools there is a connection between zonation and the joint and several action of salinity and temperature.

Submergence and emergence.—These factors may affect organisms either unfavourably, favourably, or not at all. Some of the unfavourable effects of exposure to the air have already been discussed, but it should also be remembered that there may be beneficial effects as well, as in the case of the liberation of gametes by certain brown algae, which is apparently rendered more efficient by periods of exposure to the air (S. M. Baker in ' New Phytologist ', ix, p. 54). Similarly, the effects of submergence are not necessarily beneficial. It is claimed, for instance, that certain intertidal organisms drown if submerged for too long (e.g. Colman in Journ. Mar. Biol. Assoc. U.K., xviii, p. 469, quoting Herdman), though

Broekhuysen showed that all the species of snails dealt with in his experiments could survive at least a month's continuous submergence, which was contrary to expectation for *Littorina knysnaënsis*.

Oxygen, carbon dioxide and hydrogen-ion concentration.—There is no suggestion that variations in these factors affect intertidal distribution in habitats other than rock-pools. It is well known that the oxygen content and *p*H of pools vary considerably and can be correlated with the population of any particular pool (plant-animal ratio) as well as with other factors (Stephenson, Zoond and Eyre in Journ. Exp. Biol., xi, p. 162). Although such variations might be expected to produce effects on the population in pools of certain types, we have no evidence as to whether or no they are agents of general importance for the zonation problem.

Nutritive salts.—It has already been mentioned that the distribution of these salts may well be of importance in connection with horizontal distribution in South Africa, but we have no indication that it is relevant to the question of zonation, unless it is effective in the following manner: if a plant is exposed to the air for a great deal of its life, this limits the amount of time during which it can make use of whatever phosphate and nitrate is locally available to it when it is submerged. If, on the other hand, it inhabits a rock-pool or a low level on the shore, so that it is submerged permanently or for a high proportion of its life, it can utilize the nutrient salts available much more continuously. That there is greater abundance of plant life (and, therefore, of animal life) at low levels and in pools than at high levels out of pools is on the whole true: and there may be a connection between this state of affairs and the relative *times of availability* of nutritive salts, as well as with other factors.

Light.—The possible harmful action of strong light on animals in sunlit positions in connection with the effects of desiccation, temperature and salinity has already been mentioned. This is a subject requiring further study. That there are shade-loving and sun-loving (or sun-tolerating) species is obvious, but these often become segregated into different habitats in the same zone rather than into different zones. At the same time a species which is confined to the lower levels in sunlit positions may extend to higher levels in shady places, and if shade should be extensive at these higher levels the population may be decidedly affected by this variation. In the case of shaded surfaces which are exposed to the air at low water, a reduction of desiccation and warming is involved as well as reduced light. Since, however, there may be marked differences in population at the same level, between shaded and sunlit surfaces which are permanently *submerged*, it is evident that here at least genuine light-effects are involved: desiccation is eliminated and temperature-variation reduced.

It might further be supposed that light would affect the density of population at different levels in the way postulated above for nutritive salts, but in the opposite sense—the longer an alga in a sunlit position is exposed to the air the more light it receives. This does not appear, however, to result in any general abundance of algal growth at high levels, rather the reverse—e.g., *Fucus serratus* is a densely and rapidly growing species occurring at low levels and growing much more extensively than

Pelvetia canaliculata, which receives direct illumination for a far greater proportion of its life. Evidently other factors are of more importance than light-intensity in this connection.

The dissimilar requirements of different algal species as regards the intensity and colour of light needed for optimal photosynthesis may also be effective in the present connection ; but this is perhaps more likely to account for the occurrence of many Rhodophyceae below tidemarks and in the lower and less sunlit parts of the intertidal region than to account for the zonational subdivision of the intertidal zone itself. It is noteworthy that in South Africa there is no intertidal growth of Phaeophyceae comparable in extent to the *Fucus* and *Ascophyllum* beds of Europe, but that intertidal beds of algae are often found in which prominent forms are certain species of Rhodophyceae which have their red colour more or less masked by brown ; and this fact may well be correlated with a difference between their photosynthetic powers and those of more delicate red-coloured Rhodophyceae.

Taxes.—It is known that the taxes of certain mobile animals may guide them to a suitable zone in the first instance when they are young and tend to keep them there as they grow older ; and that such movements can be modified by factors which are operative intertidally, such as desiccation and submergence. This question, however, affects the maintenance of zonation rather than its fundamental causes, and will not be discussed here.

Summary.—We have little hesitation in concluding that the principal agent responsible for the *horizontal distribution* of organisms round the South African coast is sea-temperature, that a subsidiary effect may be produced by the distribution of nutrient salts, and that no other of the factors involved has more than local effects, except in so far as it may co-operate in a minor degree with the broad variations in sea-temperature.

In connection with *zonation on the open rock* (as distinct from that in pools and shaded places) we conclude that the controllers of primary importance are the degree of exposure to the desiccation-heat-light complex acting together with the degree of exposure to wave-action. Contributing effects are undoubtedly produced by feeding habits, competition for food and space, and perhaps also by the percentage of time during which plants can utilize nutrient salts. *Local* effects can be produced by other factors, such as nature of the rock-formation and proximity of the rock to sand. Rock-formation acts primarily through its effects on degree of exposure to wave-action and distribution of shade.

The zonation in rock-pools is apparently subject to a different combination of controls from that of open rock. Here the leading factors appear to be variations in temperature and salinity with contributory effects (at present difficult to estimate) from other causes. Local effects are very powerful in the case of pools ; and selective factors are probably only markedly effective at the higher levels. The populations of pools are affected by degree of exposure to wave-action and by others of the factors controlling distribution on open rock, as well as by the variations peculiar to pools.

Light, as a primary cause of distribution, is probably more generally

effective in determining the segregation of shade-loving from surface species than in contributing to the actual zonation, though it sometimes affects the latter also, especially locally.

Although the importance of particular factors has been stressed in these paragraphs, it is clear from the information available that almost every factor whose influence between tidemarks can be imagined is able to produce *some* effect on zonation, even if this effect is not more than local in its results, or not more than contributory to other effects in its action.

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(2) SOME INTERTIDAL ENIGMAS.

By John Colman, M.A.

The work of Professor Stephenson and his colleagues during the last ten years has produced the most complete and thorough study of the shore ecology of a large region which has yet been attempted. Indeed, I know of no other ecological programme of such a detailed nature which has taken a whole sub-continent to its province. Professor Stephenson has succeeded admirably in introducing an element of reason into a distribution which could previously best be described as orderly but irrational.

Nevertheless, there are still a few points about shore ecology which I for one do not understand, and which I would like to raise.

1. *Sharpness of certain zones.*—Most intertidal species have a more or less extensive optimum part of their range, above and below which they fade out gradually. Professor Stephenson has called attention to cases where the upper limit is remarkably abrupt, the population remaining dense up to a definite level and then ceasing suddenly. This phenomenon Professor Stephenson explains in the case of *Lithothamnion* by suggesting that one gradually increasing factor, in this case desiccation, suddenly becomes lethal.

Abrupt lower limits are not so common, but there is one which merits attention because it happens to coincide with the equally sharp upper limit of another species. On the rocks around Plymouth the highest of the brown algae is *Pelvetia canaliculata*. Immediately below it comes *Fucus spiralis*. The boundary between them is remarkably precise; neither species fades out at all on approaching the limits of its domain, and neither invades the territory of the other. It is hard to see how the identical level can be lethal for two species, one in an upward sense and the other in a downward, except by a very long chance indeed; my own suggestion, that each species somehow exerts a lethal influence on its neighbour, I put very little faith in, since neither grows particularly densely and there is plenty of room for both on the otherwise bare rock.

2. *Embryology of British Littorinas.*—Of the four British Littorinas, *littorea* and *obtusata* live roughly from low-water neaps to high-water neaps, *saxatilis* from mean sea level to high-water springs, and *neritoides* mainly above high-water mark. *Littorea* sheds planktonic eggs and has a planktonic larva, *obtusata* lays egg-clusters on the fucoid weeds and the young hatch out as crawlers, having lost the velum a matter of hours before hatching; *saxatilis* is viviparous. This seemed so clear a gradation

in embryonic habit that it was assumed, by myself amongst others, that *neritoides* must also be viviparous. Actually, as Dr. Lebour has shown, *L. neritoides* lays a planktonic egg very similar to that of *littorea*. This makes it appear that the supposed embryological gradation among the Littorinas, so often cited in textbooks, has no ecological validity; instead, it seems to lend weight to the division of the genus into several subgenera, but in order to settle this point it will probably be necessary to study the embryology of the Littorinas of the world.

A second interesting point in the ecology of the British Littorinas is their distribution on both sides of the Atlantic. The only two which are natives also of the N. American shore are *obtusata* and *saxatilis*; *littorea* and *neritoides*, whose planktonic larvae might be expected to give them increased powers of dispersal, are natives only of the European side. (*L. littorea*, it is true, occurs abundantly from Nova Scotia to New Jersey, but it was deliberately introduced about 1853.)

3. *Adaptations to a littoral existence.*—Fresh-water crustacea as a general rule telescope their larval stages and reduce to a minimum the period in their life when they are at the mercy of currents and can get carried out to sea. On the shore this arrangement does not hold so generally; for example, the barnacle *Chthamalus stellatus* lives at and above high-water mark and may depend for immersion on occasional wettings by the splash of waves; nevertheless, it has as pronounced a larval existence both as nauplius and cypris as other barnacles living further down. In such a case one might reasonably expect a profound modification of the larval stages to ensure survival in such an extreme habitat, but *C. stellatus* does very well without it.

Further down the shore, near low-water mark, lives the copepod *Aspidiscus littoralis*. Here the larval stages are beautifully adapted to prevent excessive dispersal. The nauplius is limpet-shaped and looks as though built to withstand wave-action; it crawls on the weed and does not normally swim, and as a special modification is equipped with a large and powerful ventral sucker.

One wonders why, if in the case of *A. littoralis* such a thoroughgoing adaptation has been found necessary, so many other animals in a similar environment manage to get along without it.

4. *The population of* Lichina pygmaea.—The intertidal zone as a whole is remarkably rich in the number of animals living in it, sometimes belonging to rather unexpected groups; for example, around mean sea level there are actually more insect larvae to the square metre than there are in grass-land or soil. The most extraordinary population around Plymouth, however, is that living with *Lichina pygmaea*. This lichen lives above mean sea level in dark green tufts not much above an inch in height, and among its holdfasts there live fantastic numbers of the bivalve *Lasaea rubra*, the isopod *Campecopea hirsuta*, and large dipterous larvae, to the number of several hundred thousand to the square metre. I agree that larger numbers of bacteria, protozoa and nematodes can be found in muds, but these are all very minute. The population of *L. pygmaea*, on the other hand, are of a very fair size, from one-eighth to half an inch in length, and one wonders what there is in *L. pygmaea* holdfasts which makes possible the sustenance of such numbers. The hold-

fasts of other weeds on neighbouring rocks at the same level show no such populations.

5. *The relations of tidal conditions and zonation.*—Around Plymouth, the range of the tides varies from about 9 to 16 feet, and the splash zone on moderately exposed rocks is estimated to average about two feet. It seems clear, therefore, that the dominant ecological feature is the rise and fall of the tide and that the zonation must to a large extent be conditioned by it.

In many parts of the tropics, however, the tidal range is very small. Around Jamaica and among the Florida keys, for example, it does not exceed 15 inches even at springs. Furthermore, around neaps there may be no measurable tide at all for some days, and should the wind blow from some unusual quarter the general level of the sea may be raised or lowered by as much as a foot or more. Finally, since these regions are those of the trade winds, the splash zone is normally about a foot or two even on relatively sheltered beaches.

Under these conditions, then, it would be hardly surprising if intertidal zonation failed to be apparent, but this is very far from being the case. On any gently sloping stretch of beach rock on a sand-cay there will be five or six brilliantly differentiated algal zones, each with a more or less distinct fauna, each zone occupying a vertical height of not more than two or three inches. Is the rise and fall of the tide responsible here ?

These are just a few of the problems which make the seashore such a fascinating field for ecological study.

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(3) THE SIGNIFICANCE OF THE EXPOSURE FACTOR IN RELATION TO ZONATION.

By Dr. E. Marion Delf, F.L.S.

In the literature relating to marine algal zonation, there is a tendency to explain the distribution of at least the more obvious types (e.g., fucoids, laminarians) in terms of a single predominating cause, usually illumination or exposure, other factors, such as temperature, substrate, wave-action or competition, playing an altogether subsidiary role.

Emphasis on illumination as a major factor is largely based on the fact that many green and brown algae are exposed daily to much greater illumination when the tide recedes than are the majority of red ones, which are typical of the lower levels of the shore or are confined to sublittoral regions. Certain physiological investigations (Montfort in Jahrb. Wiss. Bot., LXXI, pp. 52 and 106, 1929 ; and ibid., LXXII, p. 776, 1930 ; Ehrke in ' Planta ', XIII, p. 221, 1931 ; Lampe in 'Protoplasma ', XXV, p. 543, 1935 ; and Hyde in Journ. Ecology, XXVI, p. 118, 1938) support this in that such red algae (as *Rhodymenia* and *Plocamium*) were shown to have relatively greater capacity for assimiliaton in dim light, their maximum achievement being definitely inhibited by bright light. Even with brown algae the capacity for utilization of light was sufficiently varied to suggest that light was an important factor in determining the position on the shore.

The basis for a new outlook was given by the work of Dr. Colman (in Journ. Mar. Biol. Assoc. U.K., XVIII : 1933) in his estimation of the degree of exposure integrated over a period of months for a number of common algae at Wembury, near Plymouth. Some of the species examined were confined to regions with a narrow range of exposure : for instance, *Pelvetia*, high on the shore, had a range of 70–90 per cent., but *Laminaria digitata*, at the other extreme, only occurred where the exposure was 5 per cent. or less of the total possible. The importance of the exposure factor was also emphasized by Dr. V. M. Grubb (in Journ. Ecology, xxiv, p. 392; 1935), working along somewhat similar lines at Swanage, and by Zanefeld (in Journ. Ecology, XXV, p. 431 : 1937) at Leidam, on the coast of Holland. Not the least interesting of Zanefeld's results is the comparison of the fucoids in three different localities (Leidam, Wembury and Whitecliff Bay, Isle of Wight), showing how closely in each case the zonation follows the degree of exposure.

The effects of the exposure factor have been mostly interpreted in terms of the desiccation incidental to an aërial as against an aquatic environment, and, indeed, there is some experimental evidence to support this. Zanefeld measured the rate of water loss of three species of *Fucus* and found that those occurring higher on the shore had a lower rate of water loss and a greater power of resistance to desiccation than those lower down. He believed that this resistance resided in the nature of the cell-walls. The work of Haas and his collaborators indicated also a biochemical difference in wall composition, more fatty derivatives being obtained from those with the longest periods of emergence. *Bangia*, one of the few red algae capable of enduring long exposure, also achieves drought resistance by the swelling of and water-retaining capacity of its cell-walls.

My feeling is, however, that this is too narrow an interpretation of the exposure factor, the full meaning of which requires much more investigation. For instance, there is no doubt that emergent algae are exposed to wide ranges of concentration, due to evaporation or, alternatively, to dilution by rain. In a number of algae examined by Kylin (in Ber. d. deutsch. bot. Gesellsch., 1917, p. 35) it was found that those which could endure the greatest concentration of sea water without harm were also those which could withstand the most cold. Höfler found that while some red algae (e.g. *Gigartina furcellata*) were killed by submergence in diluted sea water for only three and a half hours, others could remain unharmed for as long as two or three days, i. e. much longer than would be involved in tidal exposure. Exposure to the air also involves new conditions of metabolism—absorption of gases from the atmosphere instead of those dissolved in water, utilization of light of different composition and intensity and the effects of water-loss on the metabolic functions, a largely unexplored field.

The exposure factor is, in fact, the integration of a number of factors, some of which predominate in one locality, some in another. In the interior of a cave, as probably also in deep water, it is light which is limiting. In the flora of a cave at Bullock Island near Loch Ine, recently described (Grubb and Martin in Journ. Bot., 1937, p. 89), the mixed flora at the mouth changed towards the interior until, when the illumination was

about 0·06 per cent. of the exterior daylight (bright sun, at midday), the great majority of the remaining species were red.

In other localities temperature plays a more important part, at least in regard to certain types, as in the migrations of *Choreocolax* to deep water at Plymouth in winter (Sturch in Ann. Bot., XXXVIII, p. 27 ; 1924). In Sweden, according to Kylin, the low winter temperatures kill off the less resistant forms (*Laurencia*, *Delesseria*, *Laminaria* spp.), excepting at the lowest levels, where they have only short exposures to it. There is thus a seasonal shift of the zones occupied by these species determined by winter temperatures. In a wider sense, temperature plays a predominant part in the distribution not only (as we have heard) in S. Africa, but also in Japan (Okamura) and in New Zealand, where the southern island has subantarctic types (*Durvillea*, *Macrocystis*), whereas on the northern island (with warm currents) types such as *Xiphophora* and even species of *Caulerpa* occur.

For some years I have observed and recorded the vegetation on a solitary boulder of sandstone situated at about M.H.W.N. on the shore at Shanklin at the approach to Horsey Ledge. In 1922 there was a belt of *Fucus vesiculosus* almost round the boulder which was colonized elsewhere mainly by a growth of *Enteromorpha*. Four years later, the *Fucus* had spread upwards and laterally excepting at the apex, where the surface was covered by a fine film of a blue-green alga (a species of *Calothrix*), which peeled off in dry weather, leaving bare sandstone, and formed again in the autumn or early winter. On the south-east face this erosion was particularly marked, and extended low enough to limit the upward spread of the *Fucus*.

In June 1926 there was a marked difference between the vegetation of the seaward faces and that opposite the cliff, which was deeply shaded and bore *Fucus* only associated with *Enteromorpha* and *Rhizoclonium*. The seaward faces were exposed to brighter light and often to direct sun during low water ; yet it was on these faces that there occurred minute red algae (*Polysiphonia macrocarpa*, *Callithamnion scopulorum* and others) established in a turf of dwarf *Enteromorpha* and completely protected from desiccation by the densely overlapping thalli of *Fucus*. It seems probable that temperature was here the factor determining the differences between the sunny and the shady faces. At the present time, however, experimental investigations are greatly needed to give added meaning to observations of vegetation on the shore.

Discussion.—

Dr. G. P. Bidder offered parallels to Prof. Stephenson's observation that in still water periwinkles shut up tight and only crawl about when the water is moving. A former Zoological Secretary, E. A. Minchin, discovered in 1892 that the calcareous sponge *Clathrina clathrus*, which we had all described as without any vent—' lipostomous '—has beautifully wide vents which, in a basin of still water, shut at once into tight nipples. G. H. Parker, in 1910, found that the siliceous sponge *Stylotella* also closes its vent the moment that the water round it ceases to move. Parker gave as explanation the large quantity of suspended matter in the littoral

water inhabited by this sponge, the prompt closure of the wide vent preventing the canal system from being choked by the settling detritus. (For further details and references, see the 'Proceedings' of the Society for 21 April 1937, pp. 122, 130, 134, 143). Considering the usual environments of *Littorina*, is it not highly advantageous that it protects its gill-chamber by shutting up when the stirred mud begins to settle ?

Though among sponges many are specially modified for life between tidemarks (Bidder, 'Notes on Plymouth Sponges' in Journ. Mar. Biol. Assoc. U.K., VI, p. 376), and many do not flourish except within reach of the surge of the surface waves, the sharp horizontal line of apparent mutual exclusion, observed by Mr. Colman between the zones of two species, is not found among Plymouth littoral sponges, relative abundance altering gradually with the height above low spring tide.

It seems necessary that a horizontal dividing line must mark the threshold value of some physical quantity—light, pressure, rapidity of movement in the water, etc.—and of these hardy littoral organisms it is difficult to imagine any whose life or death by the changes in such conditions produced by one or two centimetres increase or diminution in depth.

It is, however, not quite so inconceivable in regard to their larvae. A naked flagellate or ciliate larva is a delicate thing, strongly influenced by light and absolutely requiring from the water a certain number of minutes or seconds of repose before it can fix itself and give rise to a fixed adult.

The greater part of the struggle for existence is carried on by larval forms, and this includes not only competition but destructive action. The newly hatched cuckoo secures the means of life by multiple murder, and among young organisms this is a widespread mode of morality.

In many sponges, particularly horny sponges, when the larva settles it spreads out at once into a thin disc, the most pressing duty after fixation being to obtain exclusive possession of sufficient earth surface on which to build a viable sponge. Skeleton, flagellate chambers and a canal system form themselves in the substance of the disc, and in some sponges lateral growth continues predominantly for a considerable time before vertical growth takes place. An extreme example was sent me in 1929 by the late Professor Sydney Hickson, in order to verify his belief that it was a sponge :—'It is spreading as a thin sheet over an oyster shell and over a creeping Alcyonarian growing on the shell. It comes from the Marquesas.' The flagellate chambers and fibres showed it to be a young Aplyrinid ; the thickness of the mounted fragment sent to me was about $\frac{1}{10}$ mm. and the diameter of the smothered Alcyonarian tubules was also about $\frac{1}{10}$ mm.

Let us imagine a vertical cliff whose submerged face is covered by young forms of the same creeping Alcyonarian, with a few adult Aplyrinids of this Hickson species discharging some millions of larvae in a calm 48 hours. Everywhere where the motion of the wavelets was insufficient to prevent fixation, the Aplyrinid larvae would settle and smother the young Alcyonarians, the line marking the upper limit of their settling

would be at a quite definite depth for a given size of wavelet. Above that line the Alcyonarians would flourish unassailed.

This hypothetical case indicates that when a sharp horizontal line divides the zones of two organisms, the exclusion may not be mutual. Organism A may cause the death of any organism B which ventures to the (A) side of the frontier, but B may have sanctuary beyond a certain level, not through B's own prowess, but merely because A is excluded by physical conditions of the environment.

Mr. COLMAN doubted the applicability to the fucoid algae of the instance from the sponges, cited by Dr. Bidder, where the extension over the substratum of a thin film of tissue in early life prevents the intrusion of unwelcome neighbours.

Professor T. A. STEPHENSON replied as follows.—

As I am afraid I shall be unable to be present at the next meeting, when Dr. Chapman will read his paper, but as I have had the pleasure of reading it in manuscript already, I should like to say that Dr. Chapman's contribution is of exactly the type which I hoped this discussion would evoke. It is in many ways parallel to and in agreement with the ideas I have attempted to express in my opening remarks, yet at the same time looks at the position from a different point of view and considers aspects of it which my own contribution does not. There are a number of details in Dr. Chapman's paper upon which it would be interesting to comment if there were time to do so, but under the circumstances I can mention only one or two of them. Thus Dr. Chapman's analysis emphasizes very usefully my reference to the importance of combinations of factors as well as that of isolated ones, when he shows how, at the level of mean high water of neaps, for instance, no fewer than seven of the factors which he is considering may be effective. I am also pleased to find that he confirms my own observation (described in the Society's Journal, Zoology, XL, p. 509; 1939, but not correlated with its causes) of variations in the abundance of Fucoids in relation to degree of wave action. This has also been pointed out by Fischer-Piette. I was particularly interested also in Dr. Chapman's references to different rates of tidal flow at different levels, and agree with him that these are important. Again, his examples of the lethal effect of cold (or a combination of wind and cold) on algae form a neat contrast to my own example of the effects of heat and wind in the Cape. A further point of special interest was the reference to the different rates of metabolism in submerged and emerged algae. There are other connections in which I am inclined to disagree with Dr. Chapman, but on further examination it may well prove that the disagreement is more apparent than real. Thus if I understand Dr. Chapman rightly he refers to animals as being effective as a presence-and-absence factor only; but I have quoted examples which seem to show that they can be causal and modifying in their effects also.

Dr. Colman's contribution I welcome not only on personal grounds, because of past association with Dr. Colman in ecological work, but also because it emphasizes what we all feel, that although we may claim, at the present time, that the mists obscuring the causes of zonation have begun to clear away, yet we are still very near the beginning of our search

for these causes. Dr. Colman's phrase is particularly happy when he remarks that ' Professor Stephenson has succeeded admirably in introducing an element of reason into a distribution which could previously best be described as orderly but irrational '. Nobody realizes more clearly than I do the limited and uncertain nature of the explanations we have hitherto devised, and the vastness of the territory awaiting explanation ; and if the ' element of reason ' is present in my own contribution to the subject that is quite as much as I should ever claim for it.

Dr. Delf's paper seemed to me to fall into line very well with the others, and to add reinforcement to them by a different selection of interesting details and by further reference to the complexity of the factors involved ; but I have no more specific comment to make upon it at the moment.

I should like to refer here to some points raised by Dr. D. P. Wilson, of the Plymouth Laboratory, with whom I have recently discussed zonation, and who is, unfortunately, unable to be present today. Dr. Wilson reminded me of a piece of work with which I was already familiar but which I did not mention in my opening remarks, namely, Damant's very attractive study of the bladders of *Ascophyllum*, which shows that in the case of bladder-bearing weeds at least, hydrostatic pressure may be a factor of importance in controlling the vertical distribution. Dr. Wilson also suggests, from his own observations in the Devon-Cornwall peninsula, that at certain localities where wave-action is strong there is an ecological niche unoccupied—i.e. there is a tendency for the occurrence of numerous areas of bare rock at levels which would elsewhere be well populated, apparently because of the strength of the wave-action. This forms an interesting contrast to the condition seen in South Africa, where powerful wave-action and dense population so frequently go together. A third suggestion made by Dr. Wilson is that wave-action may sometimes determine the upper limits of algae of low levels, in the sense that on slopes of certain types the amount of battering they receive in surf-beaten places will be limited in frequency and duration in the neighbourhood of low water of springs, whereas it will be much more frequent near low water of neaps, and may there act as a limiting agent. Dr. Wilson points out, lastly, that his own work on annelid larvae and that of Jägersten has shown that certain larvae are influenced to settle on particular areas of ground by the presence of the adults there, or even by sand or mud in which the adults have recently lived ; clearly this may be a factor of importance in controlling zonation. All these suggestions offer promising fields for further investigation.

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(4) ZONATION OF MARINE ALGAE ON THE SEA-SHORE.

By V. J. Chapman.

Horizontal distribution.—In my contribution to this discussion I wish to make it clear that I shall confine my attention primarily to a consideration of the factors which may control vertical zonation of marine algae on a rocky shore. In order to simplify the problems I propose further to limit my remarks to the common basic fucoid zonation, e.g. *Pelvetia canaliculata*, *Fucus spiralis*, *F. vesiculosus*, *Ascophyllum nodosum* and

F. serratus. I find myself in agreement with the opening remarks of Professor Stephenson's address and also with what he has to say about the factors controlling horizontal distribution. There would seem to be little doubt that temperature is the principal factor determining the horizontal distribution of many algal species. In addition to the South African example, quoted by Professor Stephenson, there are the shores north and south of Cape Cod, Massachussetts, and also the warm-water elements found in the algal floras of south-west England and Ireland. Around the shores of Great Britain I have not come across any tangible evidence that the distribution of nutrient salts in the water determines the horizontal occurrence of species. One example possibly worth quoting here is that investigated by Cotton (in Kew Bull. Misc. Inform., 1910, p. 15), in Belfast Lough, where the sewage outflow resulted in an extraordinary abundance of *Ulva*. It may be observed that around the mouths of large rivers, e.g. the Severn, where much silt is brought down, many species, especially red weeds, are lacking. Their absence may be due to the continual deposition of silt or to lowering of the salinity. With no direct experimental proof I should incline to the former view. The fucoids do not appear to be affected by a covering of mud to the same extent.

During the last few months I have been fortunate in having the opportunity of travelling extensively around the coast of Great Britain, and in certain places I have been impressed by the almost complete absence of fucoids, with the exception perhaps of *Pelvetia*. This phenomenon, which requires more detailed study than I have been able to give it, appears to be correlated either with the geological nature of the rock or else with exposure to strong wave action. There seems to be a tendency for the fucoid flora of calcareous rocks to be sparse, and in some places one also finds almost bare yellow sandstone. On hard rocks the bare zone is commonly populated by barnacles. Since we are confining our attention to the flora of rocky shores, it is unnecessary to point out that type of substrate, e.g. rock, sand, mud, shingle, boulders, etc., is the other principal factor controlling the horizontal distribution of seaweeds. The operation of severe exposure to wave action in eliminating some species locally, e.g. *Ascophyllum* and *Fucus vesiculosus*, can be observed on many parts of the coasts of Wales and Scotland. The reverse phenomenon, the appearance of 'surf-loving' species in areas of great wave action, can be seen on the Pacific coast of North America, where we find *Postelsia palmaeformis* forming a zone near low-water mark.

On a rocky shore, where small freshwater rivulets or streams flow out on to the beach, we find a break in the normal fucoid zonation, and instead there may be a flora composed of Chlorophyceae, principally species of *Enteromorpha*, together, in some cases, with *Fucus ceranoides*. This change constitutes a well-marked phenomenon and occurs frequently. In certain places quite large areas may be occupied by this flora, whereas in others there is merely a trickle of fresh water over the rocks with a dense mat of Chlorophyceae in the bed and extending laterally for some distance.

We may say then that temperature is the principal factor controlling the horizontal distribution on a rocky shore. The operation of this factor

constitutes a big problem, and our information is still somewhat meagre. Setchell (in Amer. Nat., LIV, p. 385; 1920) made a useful contribution towards its elucidation in his study of eurythermy and stenothermy among the algae. Plant geographers, e.g. Svedelius (in Arch. Bot., XIX, p. 1; 1924), Børgesen (in Det Kongl. Danske Vidensk. Selsk. Biol. Meddel., XI, p. 1; 1934), and Jonsson (in Bot. of Iceland, I, p. 58; Copenhagen, 1912), who have worked out the different elements, e.g. Arctic, Boreal, Mediterranean, in the floras of certain regions, have also contributed much that is of value. A good example of this type of analysis, and its results, is seen in Jonsson's work on the algal flora of Iceland. Apart from the predominating effect of temperature, the presence of much silt, the influx of fresh water with the consequent lowering of salinity, exposure to strong wave action, and perhaps (though here the evidence requires substantiation) the geological nature of the rocks, may, individually or collectively, modify the horizontal distribution of many species. It is frequently not unduly difficult to suggest which of these may be operating in any given locality.

There would seem to be little doubt that very comparable phenomena may also control the flora of rock-pools. In some districts I have visited nearly every pool is packed with *Bifurcaria tuberculata*, whilst in other places nearby the alga is completely absent. *Halidrys siliquosa* and *Gelidium corneum* only occur abundantly in pools in certain areas, whilst *Ahnfeldtia plicata* is commonly associated with sandy pools on flat shelves of rock. The factors controlling the horizontal distribution of the different elements of the rock-pool floras do not seem to be so well understood, perhaps because their investigation has not been so intensive.

Critical levels.—One would suppose that on the shore there would be certain levels above or below which the different species would not be able to grow. A very simple consideration of the tidal phenomena is sufficient to show that the conditions for the existence of living plants must be materially different at the various levels on the sea shore. Colman (in Journ. Mar. Biol. Assoc. U.K., XVIII, p. 435; 1933), in his study of zonation at Wembury, came to the conclusion that there were three such critical levels:

(*a*) Between mean and extreme low water of spring tides (annual exposure less than 5 per cent.).

(*b*) Between mean low water of neap and spring tides (annual exposure about 20 per cent.).

(*c*) At extreme (lowest) high-water mark of neap tides (annual exposure about 60 per cent.).

More recently David (Thesis for Ph.D. Aberystwyth, 1941), working on zonation at Aberystwyth, considered that there were four critical levels. We may note that only one of his levels is identical with any of Colman's. Is this discrepancy due to differences in tidal rise (Wembury, 17′: Aberystwyth, 31′), in temperature or in geological structure? At present there does not seem to be any obvious answer, and we probably shall not obtain one without further studies along the same lines.

The four levels which David believes to be important are :—

(*a*) Mean high-water mark of spring tides.
(*b*) Mean high-water mark of neap tides.
(*c*) Extreme (low) high-water mark of neap tides.
(*d*) Extreme (high) low-water mark of neap tides.

These contrary results are worth further analysis. In fig. 1 is seen an attempt to equate the zonations which have been recorded from five different localities by the use of data taken from the papers of Colman (in Journ. Mar. Biol. Assoc. U.K., XVIII, p. 435 ; 1933), Gibb (in Journ. Ecology, XXVI, p. 354 ; 1939), Grubb (ibid., XXIV, p. 392 ; 1936), and S. M. Baker (in 'New Phytologist', VIII, p. 196 ; 1909). They have all been reduced to the same datum, and although this has not proved easy I believe that the result (the figure) is substantially correct.

It is at once apparent that the weed zones in the different localities do not maintain the same levels in relation to mean low water. It might be objected that this outcome was the result of equating the work of more than one observer. We are fortunate, however, because the data for Castletown and Cumbrae are extracted from two papers by the same worker. If we compare these two alone we arrive at some very interesting results.

The *Pelvetia*+*Fucus spiralis* zone is about the same width in both localities, though it is somewhat lower at Cumbrae in relation to M.H.W.N. ; the *Ascophyllum* zone is widest at Cumbrae, whereas the *Fucus vesiculosus* belt extends the furthest vertically in the Isle of Man. The relation of the *Ascophyllum* belt to the other zones is also very striking in the two areas. Another point to be observed in the same figure is that although the tidal rise at Wembury is comparable to that at Castletown, nevertheless the respective algal zones occupy very different levels in relation to each other. In spite of these apparent anomalies, there is some very real agreement when we consider the position of the algal belts in relation to the tidal levels. It then becomes obvious that the existence of critical levels may be a reality, so much so that it is a line of enquiry that should be pursued. It would seem that the critical levels for the principal fucoids on the shore are :—

(*a*) Mean high-water neap tides.
(*b*) Extreme (lowest) high-water neap tides.
(*c*) Extreme (highest) low-water neap tides.

I cannot do more here than indicate the trend of thought. Much remains to be worked out and much is still obscure. I believe, however, that real progress can be made along these lines.

We have now to consider the operation of the factors at these critical levels. It is evident that they must function through changes which are associated with the tidal movements. The actual amplititude of the tide is evidently of minor importance. I know that one can observe perfect examples of zonation on beach rock in the Caribbean, where the tidal range is only nine inches.

Vertical zonation.—We have seen that there may be certain critical levels and that they may be important by virtue of the changes in conditions that take place in a vertical plane at or about these levels. At

this point we must be careful to distinguish between three groups of factors :

(*a*) The factors which actually determine the upper and lower limits at which any given species may grow. These we may call '*causal factors*'.

(*b*) The factors which determine whether a zone shall be present or absent in a locality. These we may term *presence or absence* factors.

(*c*) Finally, there are the *modifying factors*, which are responsible for modifying the breadth or position of a zone.

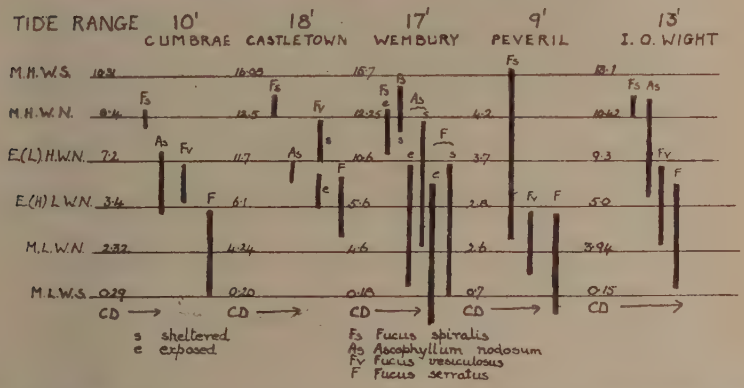

FIG. 1. Showing the relation of the principal known fucoids (at five localities) to the important tidal levels. The tide levels are represented by the horizontal lines. Underneath each locality the vertical extent of the principal fucoid zones is shown by the dark lines. Where exposure or shelter make a difference there are two lines labelled *e* and *s* respectively. On the left of each locality the Tide-table level (Chart datum) for the six tidal levels is placed opposite the respective line Above each locality is noted the maximum tidal range (based on Admiralty Tide-tables).

1. *Mechanical exposure.*—Wave action on the shore may be expected to vary according to the slope of the shore, probably being more effective on vertical than on gentle slopes. One variable is provided by changes of wind velocity during the tidal rise. An increasing wind velocity will have a greater effect at high water than at low because of the greater depth of water. This influence, however, is so variable that it cannot be expected to affect the zonation. In some areas we may find regular winds blowing, e.g. on the shores of Jamaica a strong trade wind blows every day from about 11 a.m. to 5 p.m. This, however, in so far as it may affect zonation, is essentially a *presence or absence* factor. More important will be changes in current velocity during the tidal rise and fall. Such changes may be considerable, but they will vary from place to place. In general there would appear to be little or no current operating immediately around high or low water. On the other hand, there may be a considerable water movement during ebb and flow between the

levels equivalent to ordinary high- and low-water mark of neap tides. These two levels mark quite closely the upper limit of the *Fucus spiralis* zone and the lower limit of the *Ascophyllum* zone, whilst *Fucus vesiculosus* also grows within these limits. Water movement is particularly important because the supply of dissolved gases and nutrient salts is also associated with it. Until we know more about the local inshore currents around our coasts in relation to seaweed zonation it would be difficult to say whether this is a presence or absence factor or if it is essentially causal.

2. *Substrate.*—In the vertical plane we may have :

(*a*) Geological variation in the character of the rocks. How far this will affect the zonation it is somewhat difficult to say, but observation suggests that, in general, it is not considerable. It can only operate in any case as a presence or absence factor. There is evidence that the deposition of silt or detritus provides a substrate in which sporelings of fucoids settle more readily than elsewhere, but again we are concerned with a presence or absence factor.

(*b*) Topographical variation. Here we have to distinguish between the macro- and microtopography. The latter would appear to be very important in so far as it affects colonization by sporelings, e.g. sporelings of *Fucus spiralis* are commonly confined to small cracks in the rocks. Where there are small vertical crevices in the rock the zones may be elevated, due either to capillary action, shade or protection. This is an example of a modifying factor. By macrotopography we mean changes from boulders to rock or from flat shelves of rock to steep rock, etc. Such changes, however, only determine the presence or absence of certain zones in a locality, and there is no indication that they control the limitation of any given species to a certain zone. Substrate is essentially a presence or absence factor.

(*c*) *Proximity of rock to sand.*—When the rocks are sand-covered the zonation is usually completely changed, e.g. the fucoids disappear almost completely and may be replaced by a *Cladophora-Enteromorpha-Sphacelaria* community.

3. *Submergence and emergence.*—This is really a complex of factors, some of which operate as presence or absence factors, whilst others may be truly causal.

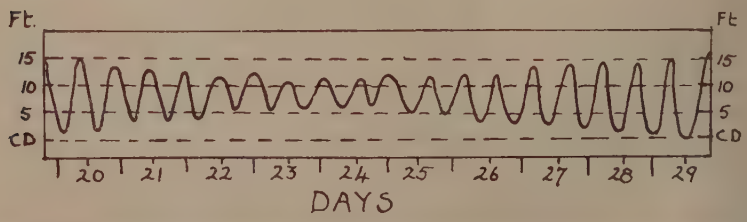

Fig. 2.—Wembury tide curves, showing intertidal and non-tidal exposure at different levels (after Colman).

(*a*) Intertidal periods. (Periods between two successive diurnal tides.) These periods increase in length with rise above mean low water. The nature of the increase can be illustrated by figures based on tidal data for levels at Wembury (after Colman, *loc. cit.*).

Level.	Tide.	Spring tide periods (hours).	Neap tide periods (hours).	Hours exposed in 1930.	Per cent. Exposure.
13	—	8·0	12·8	7241	82·7
13·25	M.H.W.N.	—	—	—	—
12·0	—	7·6	12·8	6445	73·6
11·0	—	7·2	11·6	5678	64·8
10·6	E.(L.)H.W.N.	—	—	—	—
9·0	—	6·8	7·2	4688	53·5
7·0	—	6·4	5·6	4085	46·6
6·0	—	6·2	3·0	3600	41·1
5·6	E.(H.)L.W.N.	—	—	—	—
5·0	—	6·0	0·0	2915	33·3
4·6	M.L.W.N.	—	—	—	—
4·0	—	5·6	0·0	2182	24·9

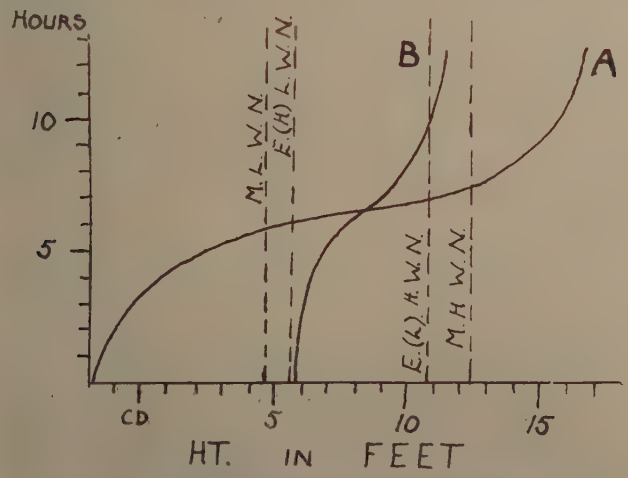

FIG. 3.—Hours of exposure during (A) spring tides and (B) neap tides at Wembury (after Colman).

It is not so much whether there is a regular change but whether, at the critical levels, there appears to be a marked change. At Wembury, during neap tides there is a distinct change between 9 and 11 feet and again between 5 and 6 feet. Between the former we have E.(L.).H.W.N. and between the latter we have E.(H.).L.W.N., both of which we believe to be critical levels.

(*b*) Non-tidal exposure. (Periods of more than one day during which no tide floods the level.)

The behaviour of this factor may also be illustrated by figures calculated from the Wembury tide-table for 1942.

Maximum period of non-tidal exposure (days)	6	4	0	0
Tide-table level	13′	M.H.W.N.	12′	11′E.(L.)H.W.N.

At 13′ there are some periods during the summer : at 12′ there are none, and all the periods are confined to the spring or autumn. Below E.(L.).H.W.N. it is never continuously dry, and above E.(H.).L.W.N. it is never continuously wet.

The periods of exposure during the summer months above M.H.W.N. must be extremely significant and may be one of the causal factors responsible for making M.H.W.N. one of the critical levels. Similarly the conditions of submergence or exposure at E.(L.).H.W.N. and E.(H.).L.W.N. strongly suggest the operation of a causal factor.

(*c*) Splash effects.—This factor operates on an exposed coast, but it cannot be causal since it merely serves to modify the level of the upper zones.

(*d*) Height of tidal rise.—We have already noticed that this only controls the width of the zones with perhaps the degree of overlap, but it cannot be regarded as a causal factor because equally good zonations occur with tidal rises of 9″ (the Caribbean), and 21′ (Aberystwyth).

(*e*) Drainage.—This factor may vary in a vertical plane because it is indirectly correlated with the angle of slope. On steeper slopes water will drain away more rapidly, both through gravity and by means of capillary action along down-hanging weed. The rocks and weed will therefore dry out more quickly on the steeper slopes. This can obviously only operate as a presence or absence factor.

(*f*) Rate of rise and fall of tide.—The rate at which the tide rises and falls varies at the different levels. It is always slow around high and low water marks and rapid in the main intertidal zone between. This phenomenon in relation to the position of the *Ascophyllum* zone has been commented upon by David (Thesis for Ph.D., Aberystwyth, 1941) and Elmhirst (in Scottish Mar. Biol. Assoc. Ann. Rep., XII, 1933). If, for example, we consider tidal movement at Wembury, it will be seen that there is nearly always a rapid rise and fall between 5 and 10′ chart datum (fig. 2). In other words, this feature is characteristic of the zone between two of our critical levels, E.(H.).L.W.N. and E.(L.).H.W.N. This suggests that here we are concerned with a causal factor.

4. *Exposure to air temperature.*—Any effect of temperature will be dependent to some extent upon slope, because on steeper slopes where the algae dry out more rapidly the longer will be the period of exposure. At Wembury distinct changes in conditions of exposure occur during neap tides at E.(L).H.W.N. and E.(H).L.W.N.; at M.L.W.N. and M.H.W.N. there are no such changes (fig. 3). Over longer periods, selected at different times of the year, the same phenomenon is apparent. As an example of a direct temperature effect there is David's observation at Aberystwyth, that sporelings of *Fucus spiralis* succumbed to prolonged cold during periods of non-tidal exposure. More recently, I have observed what may be a similar phenomenon when some low spring tides in the early morning coincided with abnormally cold weather. A gale was in force at the same time, so that excessive drying would also have occurred. As a result all the exposed *Chondrus* and *Laurencia* spp. were killed and bleached; *Gigartina stellata* was hardly affected, whilst other species, e. g., *Dumontia incrassata*, *Ulva lactuca*, *Alaria esculenta* and *Laminaria digitata*, that were exposed at extreme low water, had also suffered severely. Here we have an example of a single unfavourable factor operating at one period. In such a case it cannot be more than a modifying factor. Once more I cannot do more than draw attention to the possibilities, but near the upper limits of species there would seem little doubt that this factor may be causal.

5. *Illumination.*—In areas where there is a considerable tidal rise or where the water is permanently silty the width of the lower zones may be restricted, or theoretically the belts might even occur at slightly higher levels, because of the reduced light supply. In either event we are only concerned with a modifying factor.

Hrs. illum. in air / Hrs. illum. in sea	4·8	2·8	1·3	1·15	0·8	0·5	0·3
Tide-table level	13′ M.H.W.N.	12′	11′ E.(L).H.W.N.	9′	7′ E.(H.)L.W.	5′ M.L.W.N.	4′

Data from Wembury suggest that M.H.W.N. might be a critical level for this factor. It may be significant at other levels, but until we know more about the requirements and behaviour of the principal algae under conditions of illumination comparable to those above we are not justified in drawing any conclusions.

Changes of slope in the vertical plane may affect the degree of illumination to which a plant is exposed, but in such cases light is operating as a presence or absence factor.

6. *Salinity.*—It may be supposed that at the higher levels where there is more exposure there will be a greater daily and annual range in salinity, and hence only species with considerable tolerance to this factor will grow there. The daily range will be greater during the summer months in temperate regions, whilst it will persist throughout the year in tropical areas. It may function as a causal factor at M.H.W.N. or at E.(L).H.W.N., but until some data are forthcoming we can regard it only from a purely theoretical standpoint.

7. *Gaseous exchange and nutrient salts.*—The evidence available shows that in the marine littoral algae assimilation and respiration take place when they are submerged, and that on exposure the amount of water lost

reduces the rate of both these processes. The algae growing at high levels have, therefore, a much shorter period available for the manufacture of food materials, and in consequence they will be slow growing or else must be capable of survival under such conditions. This factor could be analysed further and could also be translated into terms of the critical levels. I believe it to be a causal factor of the first importance in determining the upper limits of species, especially near M.H.W.N.

8. *Desiccation.*—The degree of water-loss during exposure at higher levels must be one of the primary causal factors controlling the *upper*

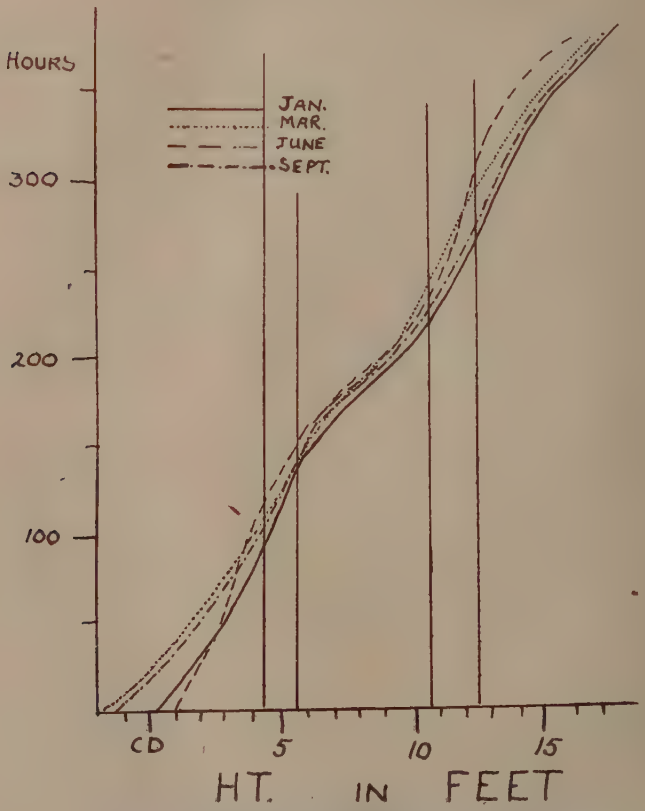

Fig. 4.—Exposure during four months at Wembury (after Colman).

limits of the species. Again it is necessary that this factor should be translated into terms of the critical levels, but this is work for the future. We have, however, to consider :—

(*a*) Water-loss during intertidal periods : this will be most serious between M.H.W.N. and M.H.W.S.

(*b*) Water-loss during the non-tidal periods; this will be important at all levels above M.H.W.N. For the principal brown seaweeds it may therefore control the upper limits of *Ascophyllum*, *Fucus spiralis* and *Pelvetia*.

(*c*) The modifying influence of exposure upon water-loss when it results in the appearance of a splash zone. Here I think we may say that we are woefully ignorant.

9. *Biota*.—Under this heading we have to consider the interaction of the animals with the plants and the inter-relations of the plants themselves. Some of the littoral animals occupy zones on the beach and by their presence will increase the competition for space, whilst at the same time they may be responsible for changes in *p*H and the chemical environment. In the case of boring animals there will be, in addition, changes in the physical environment. In the effects they exert, however, the animals will only operate as a presence or absence factor. When we consider the inter-relations of the algae there is the possibility of 'noxious' influences, such as Colman suggests, delimiting the zones. It is desirable that work should be undertaken to study this problem. Evidence from other fields suggests that such influences, rather than being harmful, are more likely to promote growth, e. g., growth substances. In the case of *Fucus* it is known that the proximity of other oospores promotes the development of rhizoids on the side adjacent to them. Furthermore, unless the limits of the species occupying the upper and lower zones relative to *Ascophyllum* are fixed, the exudation of noxious influences could not result in the uniform limits that we observe for *Ascophyllum*. Another example of inter-relations between algae is seen when rocks have been cleared; under such circumstances the first colonists are commonly Chlorophyceae, e.g., David in Wales (*op. cit.*), Hatton in France (in Bull. Lab. Marit. Saint-Servan, IX, p. 1; 1932), Bokenham in South Africa (in Ann. Natal Mus. IX, p. 47, 1938), and personal observations. The Chlorophyceae apparently provide a suitable substrate in which sporelings of fucoids can become fixed, and it has also been suggested that they provide the requisite humid environment. Here the presence of one type of weed facilitates the appearance of others. Further study will undoubtedly reveal the existence of other similar relationships.

In concluding this section we may attempt to sum up the operation of what would appear to be the primary causal factors in the following schema :—

	Inter-tidal exposure.	Non-tidal exposure.	Rate of tidal rise and fall.	Air exposure at neaps.	Air exposure Jan. and June.	Illumination submergence.	Salinity changes.	Water-loss (intertidal).	Water-loss (non-tidal).	Gaseous exchange and supply of nutrient salts.
M.H.W.N.	.	+			+	+	+	+	+	+
E.(L.)H.W.N.	+		+	+	+		+		+	
E.(H).L.W.N.	+		+	+	+					

Around M.H.W.N. it may be suggested that we are primarily concerned with problems of water-loss and growth (effects on assimilation and respiration) : at E.(L.)H.W.N. we would seem to be concerned with problems of water-loss and exposure ; whilst around E.(H.)L.W.N. we are more directly concerned with short exposures to air temperatures and with changes in rate of tidal rise and fall. I am well aware that this summary presents a much simplified picture, but in the present state of our knowledge I doubt whether an excursion into greater detail is justified.

Relation of Algal zones to tidal levels.—Under this heading I cannot hope to do more than indicate the lines along which we ought to be able to obtain further information. For my purpose I shall employ the data obtained by Colman in his work at Wembury. The relevant information is set out in the table on p. 251.

At Wembury we may note that *Ascophyllum* occupies the zone between M.H. and L.W. of neap tides. This is also the zone in which the tidal rise takes place most rapidly. We have noted previously that M.H.W.N. is a critical level, the conditions above and below being materially different. It would seem much easier to account for the upper limits than the lower. In the case of *Ascophyllum* it is possible that the inter-tidal exposure during May or June acts as a critical factor in so far as it occurs at a period when growth is at a maximum. The evidence seems to suggest that it affects the sporelings rather than the adult plant. It is difficult to see what factor or factors may control the lower limit of *Pelvetia*. It would appear that the alga is not able to tolerate too much submergence. We cannot justifiably consider that it is forced to occupy the top zone by virtue of competition, because there is no evidence that it penetrates much lower in the absence of competition. *Fucus spiralis* also occupies a zone such that it is continuously dry for long periods at a time. The perusal of this table suggests certain lines of thought regarding control of the upper limits, but it leaves us with no really adequate hypotheses about the factors determining the lower limits. We can agree with Baker (*loc. cit.*), when she says that the powers of resisting desiccation decrease in the species the lower they grow. This power of resisting desiccation can be expressed in terms of :—

(*a*) Rate of water-loss : this exhibits a gradation with the species and the level they occupy. Johnson and Skutch (in 'Ecology,' IX, p. 188 ; 1928) believed that water-loss during the most active growing period was the critical factor, but this is a point that requires further study.

(*b*) Fat content : this decreases in the species with decreasing exposure. (Haas and Hill, in Ann. Bot. XLVII, p. 55 ; 1933).

(*c*) Thickness of cell walls. This also decreases with decreasing exposure. (Zanefeld, in Journ. Ecology, XXV, p. 431 ; 1937).

The power of resisting desiccation is also reflected in the rate of growth, the upper species on the shore growing more slowly than the lower. We do not know whether these species have developed their characters as a result of the position occupied by the alga, or whether the alga occupies its position on the shore by virtue of these properties. There is no doubt, however, that there is a causal relationship. I believe that the biophysical and biochemical properties of the cells are the principal

Tide level.	Chart datum.	Alga.	Zone limit.	Per cent. exposure.	Max. period non-tidal exposure.	Mar. 14–2 hours cont. dry (max. 380).
	17 L.					
M.H.W.S.	15·91	*Pelvetia.*	Mean upper limit.	98·3	55 days.	324
	15					
	13·92	*Fucus spiralis.*	Mean upper limit.	89·6	9 days.	240
	13·78	*Pelvetia.*	Mean lower limit.	—	8 days.	
M.H.W.N.	13					
	11·89	*F. spiralis.*	Mean lower limit.	73·6	3 days.	98
	11·45	*Ascophyllum.*	Mean upper limit.	—	2 days.	
E.(L.)H.W.N.	11					
	9·82	*F. serratus.*	Mean upper limit.	58·2	0 days.	0
	9					
	8					
	7					hrs. cont. wet.
E.(H.)L.W.N.	6					
M.L.W.N.	5					
	4·47	*Ascophyllum.*	Mean lower limit.	33·3	0 days.	84
	3					
	1·90	*Lam. digitata.*	Mean upper limit.	12·1	0 days.	186
M.L.W.S.	1·0					
	0·0					
	−0·32	*F. serratus.*	Mean lower limit.	3·0	0 days.	285
	−1·0					
E.L.W.S.	−2·0					

internal factors controlling the upper limits of the species, though this again is an aspect that requires further study. It still does not help us in our search for the controlling factors at the lower limits. It is true that Johnson and Skutch (*loc. cit.*) have suggested that loss of light during the time of submergence may control the lower limits of the species. It is a possible explanation in the case of *Fucus serratus* and *Ascophyllum*, but further experimental work is necessary before we could accept this conclusion.

Colman (*loc. cit.*) would have us believe that zonation is a result of a hit-or-miss mechanism. If a sporeling settles in an environment which will suit it as an adult it will survive—if not it dies. This idea does not coincide with Gail's (in Publ. Puget Sound Biol. Stat. v, 1920) observations that the sporelings are confined to the zone they occupy as adults at a very early stage. It would seem that the critical time occurs during the sporeling phase. The nudation of areas and careful observation of the stages of recolonization, such as those carried out by David and Bokenham, may take us far towards understanding the factors controlling the lower limits. When *Ascophyllum* zones were cleared at Aberystwyth, David found that sporelings of this species only reappeared near the upper and lower limits of the zone, and that *Fucus vesiculosus* sporelings occupied the original main band. This, of course, suggests competition between *Ascophyllum* and *F. vesiculosus* ; the fact that these two species may occur in either order vertically or as a mixed community lends support to this view. A small fluctuation in one factor may determine whether *Ascophyllum* occupies the upper or lower position of the two.

Conclusions.

It is a profound regret that my present occupation, though providing me with the opportunity of observing the algal zonation in many places, has not given me so much time to digest what I have observed. For this reason much of what I have said is somewhat disconnected ; nor have I had the opportunity of working out lines of thought to the extent that I could have wished. The more I see of the algae on the shore the less I feel I know about them and why they occupy the zones they do. We can find one area in which a certain factor would seem to control zonation, only to find that in an adjacent area the same factor appears to have no effect. Certain obvious factors are conspicuous, but they are primarily presence or absence factors and not causal. I believe that we do understand something about the causal factors controlling the upper limits of certain species, but we seem far from realizing those responsible for determining the lower limits.

I think that further progress may be obtained by :—

1. Studies in which the algae and tidal factors are analysed, e. g., studies comparable to those of Colman, Grubb, and of myself (in Journ. Ecology, xxxi, p. 147 ; xxvii, p. 60 ; xxviii, p. 118 ; and xxix, p. 69, 1938–41), and of Johnson and York (in Publ. Carnegie Instit. Wash. no. 206 ; 1915). Particular attention needs to be paid to the existence of critical levels.

2. Extensive experiments in which areas of rock are completely bared. These should be conducted under as many different environmental conditions as possible. The process of recolonization may then shed light on the basic zonation, e. g., the fucoids. If we could fully understand that we should have achieved much.

THE ENTOMOSTRACA OF THE BOTTOM DEPOSITS OF WINDERMERE.

By D. J. Scourfield, I.S.O., F.L.S., F.R.M.S.

In an article published in 'Nature' last year by Jenkin, Mortimer and Pennington ('The Study of Lake Deposits', 'Nature', cxlvii, p. 496; 1941), some account was given of the means by which cores have been obtained from the bottom deposits of Windermere, together with some details of the cores themselves and the results of their examination for plant and animal remains. In the present paper it is proposed to give fuller details of these results so far as they relate to the Entomostraca.

The search for the remains of these little Crustaceans in the cores was carried out in the following simple way. Small samples of the still wet deposits, usually three or four from different levels of each core examined, were placed in clean flasks with distilled water and vigorously shaken. When the resulting muddy liquid had settled somewhat, some of the loose material was taken from the bottom of the flask with a clean pipette and spread out on a glass plate for examination under the microscope. Several such spreads were examined from each sample and thirteen separate cores were tested in this way ranging from deposits in shallow water (4 to 7·8 metres) to those in the deepest part of the lake (65·5 metres). It may be mentioned here that generally speaking the cores consisted mainly of a dark brown organic deposit (2·5 to 4 m.), the 'brown mud' of the paper already referred to, resting upon pink laminated glacial clay (1 m. and over). The semi-liquid 'surface ooze' (5 to 20 cm.) was not regarded as forming part of a core.

Altogether twenty-four species of Entomostraca were definitely noted, all except one belonging to the Cladocera. Strangely enough no remains of Copepods and only a single specimen of an Ostracod were seen. With the exception of a single *Bosmina obtusirostris*, no complete specimens were found, the remains being usually confined to separated and empty valves and head-shields, or to detached post-abdomens, mandibles, claws, setae, etc. Occasionally, however, mandibles were found associated with head-shields (mostly in the case of *Bosmina*), and more rarely post-abdomens or even a few of the feet occurred inside the valves. Complete details of the parts recognized are given under the notes on the species.

By far the most numerous and most frequently occurring remains, being found, in fact, in every sample yielding any animal remains, were those of the planktonic *Bosmina*. Remains of three other planktonic forms, viz., *Daphnia* sp. (*longispina-hyalina* type), *Bythotrephes longimanus* (most probably) and *Leptodora kindti* were also obtained, but were not very numerous. All the other species represented were essentially littoral forms, in the case of the Cladocera all belonging to the family Chydoridae. Presumably these had been washed from the marginal areas into the

open water, most likely during stormy weather, or had been brought into the lake by the rivers, although a few may possibly have been living at the bottom, at least in the case of the shallower water deposits.

It is noteworthy that, although head-shields and valves of *Bosmina* were comparatively abundant, no trace of similar parts of *Daphnia* was found. It may be that the chitin of the shell of *Bosmina* differs from that of *Daphnia* in being more resistant to decomposition, but even so it is surprising that of the myriads of cast skins of *Daphnia* which must be continuously raining down from the upper waters, none should have been found in the bottom deposits. It is, of course, equally or even more surprising that no remains of the planktonic or any other Copepods should have been found and only one specimen of an Ostracod.

In the majority of cases the remains could be definitely identified with existing British species, all of which, moreover, with one or possibly two exceptions, had already been recorded as living in the lake at the present day. In the cases where specific determination was not possible owing to lack of critical details, the probability therefore, seems to be that they also were identical with species now occurring in the lake. No evidence was forthcoming of the existence of any of the few forms of Cladocera peculiar to extreme northern or sub-arctic conditions.

Most of the Cladoceran valves seen belonged to the usual parthenogenetic females, but evidence of the existence of sexual forms was furnished by the finding of the valves with enclosed appendages of a male *Alona rectangula* and a male *Chydorus piger*, also the detached male antennules of *Bosmina* and various ephippia (i. e., the protecting coverings of the so-called ' resting ' or ' winter eggs '). The ephippia belonged to *Bosmina* and to three species of *Alona*.

So far as can be judged from the records at present available, the Cladoceran fauna of Windermere has not altered very much, if at all, since these animals first made their appearance in the lake after the glacial period. The thin layer of organic material near the middle of the basal bed of laminated clay shown in the core from the deposit in rather shallow water of 7·8 metres, is believed to be the oldest deposit containing remains of plants and animals, and the species of Entomostraca recorded from that layer all occur in the main bed of organic material, i.e., in the ' brown mud ' above the clay. They are also living in the lake at the present day. No trace of Entomostraca has been seen in either the lower or upper portion of the laminated clay in this core or in the clays from the other cores.

The only difference noticed which approached or possibly amounted to one of specific rank between the forms found in the cores and those now occurring in the lake was in the case of *Bosmina*. Most of these could undoubtedly be classed as *B. obtusirostris* as at present, but side by side with them were found forms in most cores which could only be regarded as *B. longispina* s. str. Unfortunately, the exact status and significance of these large long-spined *Bosminas* is uncertain, but their presence probably does point to a less evolved condition of the lake than at present. Further remarks on the subject will be found in the detailed notes on the species.

No essential difference was noticeable between the shallow water and deep water cores.

As might have been anticipated, various references to the occurrence of Entomostraca are to be found in the accounts of previous work on lake deposits. For instance, Conger ('The Contribution of Diatoms to the sediments of Crystal Lake, Vilas County, Wisconsin', in Amer. Journ. Sci., CCXXXVII, pp. 324–40 ; 1939) in the general description of the samples of cores from Crystal Lake, Wisconsin, mentions that they contained Crustacean remains without, however, giving any particulars. Lundquist ('Bodenablungerungen und Entwicklungstypen der Seen' in 'Die Binnengewässer,' II ; 1927) in the description of several of the plates in his book showing remains of these animals usually refers to them simply as 'Cladocerenschalen', but in one instance gives the genus as *Lynceus* (=*Alona*). In passing it may be noted that this particular specimen (Plate II.) is the post-abdomen of either *Alona quadrangularis* or *A. affinis* and that it is without the claws, just as was found to be the case in the Windermere deposits. Again, Groschopf ('Die postglaziale Entwicklung des Grossen Plöner Sees in Ostholstein auf Grund pollenanalytischer Sedimentuntersuchungen', in Archiv f. Hydrobiologie, XXX, pp. 1–84 ; 1936), in a work dealing mainly with the pollen found in the bottom deposits of the Grosser Plöner See, incidentally mentions the occurrence of various parts of *Daphnia*, *Bosmina* and other Cladocera, including an ephippium of *Daphnia* sp. He also records the finding of the antennae of Copepods. But, so far as I am aware, the present report is the first in which a fairly large number of Entomostraca have been specifically identified in the cores from lake deposits *.

* Shortly after the reading of this paper my attention was drawn to another and very important contribution to our knowledge of the animal remains in lake deposits, which had recently been published, by E. S. Deevey, Jr. ("Studies on Connecticut Lake Sediments : III. The Biostratonomy of Linsley Pond," in Amer. Journ. Sci. CCXL, pp. 233–264 and 313–324, 1942), with an appendix by T. S. Austin ("The fossil species of *Bosmina*" (*loc. cit.* pp. 325–331)). It appears that altogether seven species of Cladocera were noted in the cores from the bottom deposits of Linsley Pond, viz., *Bosmina longispina* (probably *obtusirostris* form) (H, P, V.), *B. longirostris* (H, V.), *Eurycercus lamellatus* (P.), *Alona quadrangularis* (P, V.), *A. affinis* (P.), *Leydigia quadrangularis* (P.) and *Chydorus faviformis* (V.) It is most interesting to learn that, as in Windermere, the remains of *Bosmina* were much the most abundant, and in this connection reference is made to a paper by E. Wasmund ("Bitumen Sapropel and Gyttja" in Geol. Fören. Stockholm, Förh. LII, pp. 315–350, 1930) in which it is said that this special resistance of the chitin of *Bosmina* to decay had already been noted. Again, as in Windermere, no remains of Copepods were found and apparently none of Ostracods. Other animal remains included parts of Insects, statoblasts of Polyzoa, Sponge spicules, etc. Reference is also made to a paper by I. I. Messiatzev ("Die fossile Fauna der Seen in Kossino" in Arb. Biol. Stat. Kossino, I, pp. 16–26, 35, 1924) in which, it is stated, fifteen species of Cladocera were recorded from deposits in three Russian lakes in the vicinity of Moscow.

It is to be noted that in the work on the Linsley Pond sediments an attempt was made not only to identify specifically as far as possible the remains of Cladocera and other animals found, but to get some idea of their relative abundance at different levels in the deposits by actual counting of the specimens in definite quantities of material. One result, shown by the Chironomid remains at any rate, was the proof that "the early lake was qualitatively as well as quantitatively oligotrophic". [April, 1943.]

Notes on the Species.

The following letters in brackets after each species indicate the separate remains found :—A, antennules ; C, terminal claws ; E, ephippia ; F, filtering combs of legs ; H, head-shields ; M, mandibles ; P, post-abdomens ; S, setae ; V, valves. The number following denotes the number of samples in which the species was found. The total number of samples examined, apart from the clays, was thirty-three.

Daphnia sp., *longispina-hyalina* type. (C, F, M.) 21. Terminal claws of a *Daphnia*, usually associated with a few of the anal teeth, occurred many times ; also a few isolated filtering combs and mandibles probably belonging to the same species. The claws were finely ciliated along their whole length, but without combs. They evidently belonged to a form either identical with, or very closely allied to, the *galeata* variety of *D. hyalina*, the present form in Windermere, but whether they were actually *galeata* cannot be stated as no head-shields or valves were found.

Bosmina obtusirostris and ? longispina sensu stricto. (A, E, H, P, V.) 33. Empty valves and head-shields of *Bosmina* were more or less abundant in all samples. They were all of the *longispina-obtusirostris* type, and this was confirmed by the claws on the few detached post-abdomens seen. The majority were evidently forms of *B. obtusirostris* such as occur in the lake at present. In addition to these, however, there were also present in about half the samples, more particularly from the middle parts of the deposits, rather large forms with shell-spines from one-third to nearly half the valve length and rather long slightly curved antennules. Most of these could, with little doubt, be regarded either as *B. longispina* s. str., or something very close to it. Such forms do not seem to occur in the lake at the present time, but as the specific distinction between *B. longispina* and *B. obtusirostris* is by no means sharply defined and all species and varieties of the genus are subject to much variation, the significance of the presence of these forms in the cores is somewhat uncertain. As, however, *longispina* forms occur in some less evolved lakes at the present time, e.g., Wastwater, it is probable that their presence in Windermere in former times is to be correlated with the less evolved conditions then prevailing in the lake. Ephippia of *Bosmina* (see Lilljeborg, ' Cladocera Sueciae ', in Nov. Acta Reg. Soc. Sci. Upsal. Ser. 3, xix, 1900, Pl. xxxiii, fig. 5, and Scourfield,' The Ephippium of *Bosmina* ', in Journ. Quekett Microsc. Club, Ser. 2, viii, pp. 51–56 ; 1901). In one case the egg itself was inside and appeared in fairly good condition. This, however, was from near the top of a core. The very characteristic male antennules were found on two occasions.

Eurycercus lamellatus. (A, C, H, P, V.) 15. The post-abdomens were without claws, and this was usually the case in all the other species where such organs were found detached. Detached claws, however, were seen on two occasions, and the distal part of the very characteristic antennule several times. None of the specimens gave any indication that they belonged to *E. glacialis*, and it has consequently been assumed that they all belonged to the common species *E. lamellatus*.

Camptocercus rectirostris. (P, V.) 14. Most of the valves seen still showed the fine scratch-like markings between the main parallel lines. The post-abdomens were definitely of the *rectirostris* type, but, as

so commonly the case with these structures when found detached, they were minus the claws.

ALONOPSIS ELONGATA. (V.) 5. The valves were unmistakable, even the fine striae between the oblique lines being visible.

GRAPTOLEBERIS TESTUDINARIA. (H, V.) 11. The very characteristic head-shields and valves of this species were quite easily recognized.

ALONA AFFINIS. (C, E, P, V.) 25 ? There is a possibility that some of the remains recorded under this name may have belonged to *A. quadrangularis*. But in most cases the very fine striping characteristic of the valves of *A. affinis* was seen, and in one or two detached claws the basal spine was ciliated as is usual in this species. The post-abdomens were minus the claws. One ephippium was found. It agreed with that described and figured (fig. 12) in my paper on 'The Ephippia of the Lynceid Entomostraca' (Scourfield in Journ. Quekett Microsc. Club, Ser. 2, VIII, pp. 217–44 ; 1902). Over the darkened part, the fine striae and pittings could be made out and the posterior ventral areas of the valves were retained as part of the ephippium.

ALONA QUADRANGULARIS. (P, V.) 1 ? As already mentioned, some of the records under *A. affinis* may have been *A. quadrangularis*, but only one specimen was seen which was definitely taken to be this species. In this case the post-abdomen was enclosed in the valves.

ALONA COSTATA. (E, P, V.) 3+1 ? Ephippia of this species were seen in two samples from a shallow water core. They closely resembled fig. 15 in the paper quoted under *A. affinis*. In two cases the posterior corners of the valves were retained, but in another they were not. The vertical striping was well marked and some inner membranes were still present. The detached post-abdomen was without claws. This species has not hitherto been recorded as living in Windermere at the present time, but its actual absence is very improbable.

ALONA RECTANGULA. (E, P, V.) 6+5 ? The ephippium seen was exactly as shown in fig. 16 of the before-mentioned paper, including the characterisitc 'packing', but the ventral margins of the valves and the egg were naturally absent. The only post-abdomen of a female seen occurred inside a specimen of the valves. It was typical of the species and still retained the claws. A male was represented by valves which very fortunately still enclosed the feet and post-abdomen. The characteristic hook on the first pair of feet was quite evident, and the post-abdomen, although without the claws, was typical of the species.

ALONA GUTTATA. (V.) 7. In all the specimens seen the lines of small tubercles (guttae) were well marked.

RHYNCHOTALONA FALCATA. (P.) 1. Two specimens of the post-abdomen of this species were seen in one sample. They were without the claws, but otherwise were characteristic of the species.

ALONELLA EXCISA. (V.) 11. The valves showed the fine striae within the hexagonal markings peculiar to this species.

ALONELLA EXIGUA. (V.) 6. No striae within the markings were visible in the specimens referred to this species. In one case at least the straight, i. e., not bayed, ventral margin was also quite evident.

ALONELLA NANA. (H, V.) 13. The remains were mostly valves of this minute and very strikingly marked species, but a head-shield was recognized once.

PERACANTHA TRUNCATA (V.) 1. Only the posterior part of the valves of a single specimen was seen. There were about sixteen somewhat irregular teeth on the posterior margin.

CHYDORUS GLOBOSUS. (V.) 1. Only one valve (half-shell) of this species was seen. It was from a shallow water core and showed the valve sculpture and the characteristic central patch of dark brown as plainly as in a recent specimen.

CHYDORUS SPHAERICUS. (V.) 10. It is rather surprising that this exceedingly common species should have been found in only ten samples. Specimens were most numerous in the layer of organic material in the laminated clay, i. e., in the presumed oldest organic deposit, and in these the usual delicate hexagonal network covering the valves could be made out almost as well as in present day examples.

CHYDORUS PIGER. (V.) 23. The valves could be identified by the dense fringe of setae on the posterior part of the ventral margin, and some showed evident rows of tubercles and also the minute pitting of the chitin as is usual in recent specimens. A male was indicated by the presence of a hook from one of the first pair of feet still remaining inside the shell.

ANCHISTROPUS EMARGINATUS. (V.) 1. Only the ventral portion of one valve was found, but it showed the characteristic structure of this part quite clearly.

BYTHOTREPHES LONGIMANUS (most probably). (M, S.) 20. The very peculiar mandibles of a *Bythotrephes* were found in a number of samples from both the shallow and deep water cores. They were exactly similar to the figure by Lilljeborg (see Lilljeborg, 1900, Pl. lxxx, fig. 15), and it is assumed that they belonged to *B. longimanus* rather than to the very rare *B. cederströmi*. A few detached terminal setae of the first pair of legs and also some of the terminal segments of the same pair were seen. They could be recognized by certain characteristic details of structure.

LEPTODORA KINDTI. (M.) 2. The presence of this species in the deposits was revealed by the finding of two mandibles. These organs are most characteristic (see Lilljeborg, 1900, Pl. lxxxvii, fig. 7), and are no doubt by far the hardest part of this most delicate and transparent organism. In one case it was only the distal half of the mandible that was found, but the details of structure, including the little process marked '*b*,' by Lilljeborg, were typically developed.

? CYPRIA OPHTHALMICA. (V.) 1. Only a single specimen of an Ostracod was found during the whole course of the examination of the deposits. It was an empty shell though both valves were present. Judging by its size, shape and apparent thinness and transparency it probably belonged to the very common *Cypria ophthalmica*.

Addendum on other animal remains seen in the deposits.—During the search for Entomostraca a good many fragments of Insects were seen, more particularly parts of *Chironomus* larvae, and on two or three occasions remains of small mites were noted. Rhizopod tests occurred in all samples, and altogether representatives of the following genera were recorded :—*Arcella*, *Centropyxis*, *Difflugia*, *Lesquereusia*, *Euglypha*, *Heleopera*, *Hyalosphenia*, *Nebela*, *Paulinella*, *Quadrula* and *Trinema*, but the species were not determined.

AQUILEGIA EINSELEANA SCHULTZ FORMA SCHLEICHERI FORMA NOVA.

By M. Skalińska, Ph.D. (Warsaw).

The specific name *Aquilegia viscosa* has been applied to a number of quite different forms which are now recognized as separate species : *Aquilegia viscosa* Gouan includes not only the small-flowered species from Lozère, Gard, Hérault, Aveyron and Pyrenées Orientales, but also *A. vulgaris* var. *viscosa*. Specimens of *A. Einseleana* Schultz (=*A. Bauhini* Schott, *A. pyrenaica* Koch) have also sometimes been labelled *A. viscosa* Gouan (e.g., exsiccata of Facchini from Tyrol and of Jabornegg from Carinthia), or *A. viscosa* DC., or *A. viscosa* Reichb. *A. viscosa* Waldst. and Kit. (*A. Kitaibelii* Schott) represents a separate species native in Croatia and Dalmatia. A different *A. viscosa* was described by I. Gaudin ('Flora Helvetica,' III, pp. 477–8; 1828) in connection with *A. pyrenaica* DC. and *A. viscosa* Gouan. Its description is based upon exsiccata of Schleicher and Thomas ; however, it is doubtful whether the plants collected by Schleicher above Lugano and by Thomas in the vicinity of Como and of Bellano really represent the same form ; it is probable that the exsiccata of Thomas represent *A. Einseleana*, which is a calcicolous species widely spread over the southern calcareous border of the eastern Alps ; its chief area extends from Carinthia and Carniolia through Tyrol, the Vicent Alps, the Venezian Alps and Lake Garda to Lake Como : the western limit of its area includes the western border of Lake Como (Majolica, Monte San Martino). It should be remarked, however, that the description given by Gaudin for this '*A. viscosa*' does not agree in some details with the features of *A. Einseleana* (e.g., the shape of the leaflets and of the laminae of the petals) ; it corresponds to the specimens of Schleicher originating from Italian Switzerland. According to Gaudin, these plants were collected above Lugano, in the Canton of Tessin, where the occurrence of *A. Einseleana* has not been established with certainty ; it has been recorded by some authors and queried by others. Moritzi ('Die Pflanzen der Schweiz,' p. 287 ; 1832) recorded *A. pyrenaica* from the mountains of Italian Switzerland ; this is, of course, not *A. pyrenaica* DC. ; *A. Einseleana* was often recorded as *A. pyrenaica* from the south-eastern Alps before being named by Schultz in 1848. Gremli also recorded *A. pyrenaica* DC., from Tessin, in the first edition of his 'Excursionsflora' (1867, pp. 74, 75) ; in the second edition (1874, p. 76), however, he corrected his previous record and mentioned *A. Bauhini* Schott (*A. pyrenaica* Gr. non DC.), from the lake of Como only, and as no longer occurring in Tessin. On the other hand, Christ (Flore de la Suisse et ses origines, transl. E. Tieche, ed. of 1907, p. 49) mentioned *A. Einseleana* among plants which grow on calcareous soil and limestone in the Lugano district. Schroeter (Flora des Südens d.h. Insubriens, südl. Tessin u. Oberitalienische Seen, p. 96 ; 1936), on the contrary, denies categorically its occurrence in Tessin : 'In Tessin fehlt sie ; die früheren Angaben von Generoso und S. Giorgio beruhen auf der Verwechslung mit einer zarten Abart von *A. vulgaris* (var. *salvatoriana* Cheneward' (pp. 96, 97). Concerning this last opinion, however, it should

be remarked that *A. vulgaris* var. *salvatoriana* is, according to the description, a dwarf form of *A. vulgaris* ; it has distinctly hooked spurs and therefore can be easily distinguished from *A. Einseleana*, the spurs of which are very short, thin, and nearly straight.

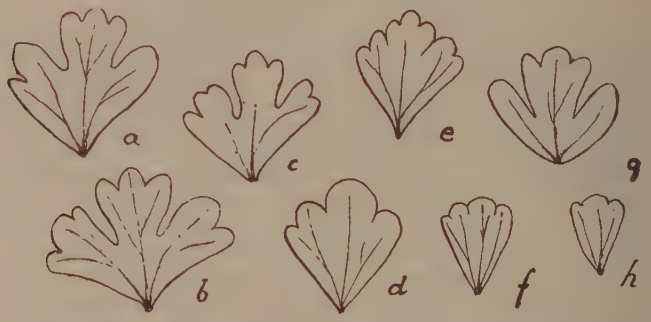

Fig. 1.—Middle leaflets of basal leaves : *a–c*, *Aquilegia Einseleana* forma *Schleicheri* ; *d–h*, forma *typica* [*d*, specimen from Bavaria ; *e*, from Como ; *f*, from Garda ; *g*, *h*, from Tyrol]. All leaflets belong to biternate leaves with the exception of *g*, which represents a leaflet of a ternate leaf ; thus, its middle lobe only, not the whole leaflet, corresponds to the medium leaflets of *d*, *e*, *f*, *h*. Natural size.

Evidently the above records do not enable us to solve the problem what species the '*A. viscosa*' collected by Schleicher near Lugano represents. I have had the opportunity of studying in the Kew Herbarium three of

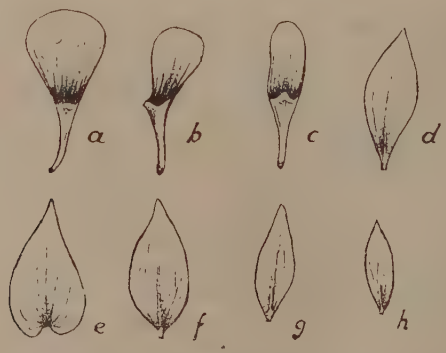

Fig. 2.—Petals and sepals of *Aquilegia Einseleana* forma *Schleicheri* (*a*, *e*), and forma *typica* (*b*, *d*, from Como ; *c*, *g*, *h*, from Tyrol ; *f*, from Carinthia). Natural size.

Schleicher's specimens determined as *A. viscosa*. A detailed comparison of these plants with various specimens of *A. Einseleana* shows that these plants are not identical with this species in spite of some degree of

similarity. The first specimen is the most robust of the three plants ; it is labelled primarily ' *Aquilegia viscosa* L.' with the addition ' Suisse italienne ' ; on a separate label there is the remark : ' Jardin de Schleicher, 4 Juillet 1809 ' ; perhaps this plant represents a cultivated specimen. The second specimen is signed by Schleicher, though no details concerning the locality are given. The third has only the remark ' Ex Helvetia misit Schleicher 1818 '. Judging from the description given by Gaudin, it seems very probable that these specimens represent plants recorded by him as being collected above Lugano ; as mentioned above, the plants of Schleicher cannot be identified with *A. Einseleana* ; the chief differences concern the shape of the leaflets (see fig. 1) and that of the sepals and petal laminae (see fig. 2) ; the plants were found beyond the area of *A. Einseleana*, although close to the western limit of its range. Owing to these differences in morphology and geographical distribution, the plants from Italian Switzerland deserve to be considered as a separate form of *A. Einseleana* ; I name this form *A. Einseleana* forma *Schleicheri*.

The species *A. Einseleana* includes, besides forma *typica*, three other forms : forma *Portae* (Huter) Gürke ; forma *thalictrifolia* (Schott et Kotschy) Fiori ; forma *pseudothalictrifolia* Pampanini (' Flora Italica exsiccata ' Nuovo Giorn. Bot. Ital., N. Ser. XIII, pp. 42, 43 ; 1906) ; they all occur as endemics westward of Lake Garda, within the area of *A. Einseleana* forma *typica*. The morphological differences between these forms and forma *typica* are not more sharply expressed than those existing between forma *typica* and forma *Schleicheri*. The Latin diagnosis and the description of the new form follow :—

Aquilegia Einseleana Schultz forma *Schleicheri* forma nov., foliolis majoribus multo latioribus magis incisis, praeterea sepalorum et petalorum forma a forma *typica* distincta.

Folia radicalia biternata ; foliola lata, basim versus late cuneata, ad medium trilobata, incisa, lobis 6–8 rotundis distantibus, lobo medio 14–23 mm. longo 17–28 mm. lato ; foliola supra glabra, subtus puberula. *Sepala* ciliolata, ovata, circa 20 mm. longa, 11 mm. lata ; *Laminae petalorum* amplae, ad apicem rotundatae, 14–16 mm. longae, 9–13 mm. latae, sepalis paulo breviores. *Calcaria* gracilia, brevia, recta, laminis multo breviora. *Stamina* laminis petalorum aequilonga.

The flowering stem attains the average height of *A. Einseleana* forma *typica* (25–35 cm.) and corresponds with this form also in its branching. *The basal leaves* differ distinctly from those of forma *typica*, they are biternate, while forma *typica* has biternate or ternate leaves ; the leaflets are usually sessile, larger and much broader than in forma *typica* ; they are more compound in outline (see fig. 1 *a*, *b*, *c*) ; they are 14–23 mm. long, 17–28 mm. wide, thus, their length is exceeded by their width, while in forma *typica* they are rather elongated (10–22 mm. long and 8–16 mm. wide). The leaflets of forma *Schleicheri* are trilobed owing to two main incisions which extend to half their length, being deeper and much broader than in forma *typica* ; additional shallow and rather broad incisions divide each of the three lobes into 2–3 rounded lobules ; their total number is 6–8 ; in biternate leaves of forma *typica* (fig. 1 *d*, *e*, *f*, *h*) the leaflets are also trilobed, both the main and the additional incisions are, however, narrow and shallow ; there is usually only one additional incision per lobe, or they are not present at all ; thus the number of lobules

is lower on the average than in forma *Schleicheri* (3–6), attaining only rarely 7 or 8 ; ternate leaves of forma *typica* have leaflets still less compound in outline (fig. 1 *g*). It should be remarked that the leaflets of forma *Schleicheri* are similar in size and general shape to those of forma *Portae*, which occurs as an endemic on Monte Cornablacca, above Val di Sabbia, westward of Lake Garda. *The stem-leaves* are reduced. In the pubescence of the leaves, forma *Schleicheri* corresponds to forma *typica* : the leaflets are glabrous on their upper surface and sparingly pubescent beneath ; on the other hand, the three remaining forms within the species : forma *thalictrifolia*, forma *pseudothalictrifolia*, and forma *Portae* have leaflets pubescent on both surfaces.

The flower.—The diameter of the flowers reaches 40 mm. ; thus the flowers correspond in their size to larger flowers of forma *typica*. The sepals (fig. 2 *e*) are acuminate and attain their greatest width near the base ; they differ in shape from those of forma *typica* (fig. 2 *d*, *f*, *g*, *h*), whose sepals have their greatest width near the middle ; the length of the sepals is in forma *Schleicheri* 20 mm., the greatest width is 11 mm., while in forma *typica* they are 13–22 mm. long and 4–10 mm. wide. The total length of the petals of forma *Schleicheri* attains 23–26 mm., exceeding that of forma *typica* (17–22 mm.) ; this is due to a remarkable enlargement of the size of the laminae (fig. 2 *a*) ; this detail gives the most distinct difference, connected with the shape of the flower, from forma *typica* (fig. 2 *b*, *c*) ; on the other hand, the length of the spurs is nearly the same in both forms. The laminae are rounded at the apex, equalling the stamens in length ; they are 14–16 mm. long, and 9–13 mm. wide, while those of forma *typica* are only 10–12 mm. long and 4–9 mm. wide. As in forma *typica*, the spurs are thin, short, and almost straight.

Table I. summarizes the differences between forma *typica*, forma *Schleicheri*, and forma *Portae*.

TABLE I.—Differences between *A. Einseleana*, forma *typica*, forma *Schleicheri*, and forma *Portae*.

	Forma *typica*.	Forma *Schleicheri*.	Forma *Portae*.
Basal leaves	Biternate or ternate.	Biternate.	Biternate.
Middle leaflets : length	10–22 mm.	14–23 mm.	18–23 mm.
width	8–16 mm.	17–28 mm.	22–26 mm.
Number of lobules	3–6 (–8)	6–8	5–10
Pubescence : upper surface	Glabrous.	Glabrous.	Pubescent.
lower surface	Sparingly pubescent.	Sparingly pubescent.	Pubescent.
Flower : diameter	25–40 mm.	About 40 mm.	35–44 mm.
Sepals : length	13–22 mm.	20 mm.	17–22 mm.
greatest width	4–10 mm.	11 mm.	7–9 mm.
Petals : total length	17–23 mm.	23–26 mm.	18–23 mm.
length of laminae	10–13 mm.	14–16 mm.	11–13 mm.
width of laminae	4–9 mm.	9–13 mm.	8–10 mm.
length of spurs	7–10 mm.	9–10 mm.	7–10 mm.

Concerning the origin of forma *Schleicheri*, it seems probable that it may have evolved from *A. Einseleana* by the process of intraspecific differentiation. The three previously described forms: forma *Portae*, forma *thalictrifolia*, and forma *pseudothalictrifolia* differ from forma *typica* in a number of characters; these differences are purely genic, thus the process of differentiation within the species has been due presumably to gene mutations. The comparison of the characters of forma *Schleicheri* with forma *typica* favours the assumption that this form arose in the same way; however, it should be emphasized that none of the three other forms has advanced beyond the area of forma *typica*, whereas forma *Schleicheri* was collected just westward of the area of forma *typica*, where it occurs above Lugano in Italian Switzerland.

I wish to express my deep indebtedness to the late Sir Arthur Hill, Director of the Royal Botanic Gardens, Kew, for granting me facilities to continue my research work away from Poland.

A REVISION OF THE INDIAN AND BURMESE SPECIES OF SAGERAEA (ANNONACEAE).

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The Annonaceous genus *Sageraea* was first described by Dalzell, in 1851, based on an elegant laurel-like tree from Bombay. A somewhat similar genus, *Bocagea* St.-Hil., which may be regarded as the New World counterpart of *Sageraea*, had been described earlier in 1825. Hooker and Thomson in their 'Flora Indica' recognized *Sageraea*, but in their subsequent treatment of the Annonaceae ascribed the Indian species of *Sageraea* to *Bocagea*. Unfortunately they did not give any definite reason for not keeping *Sageraea* distinct from *Bocagea*. In 1893 King again separated *Sageraea* from its allied American genus, but later Cooke, in his 'Flora of Bombay' (1, p. 17), treated the Indian species under *Bocagea*. Later authors like Prain, Gamble and Craib have recognized the East Asiatic species as generically distinct from the New World species of the seemingly allied genus *Bocagea*.

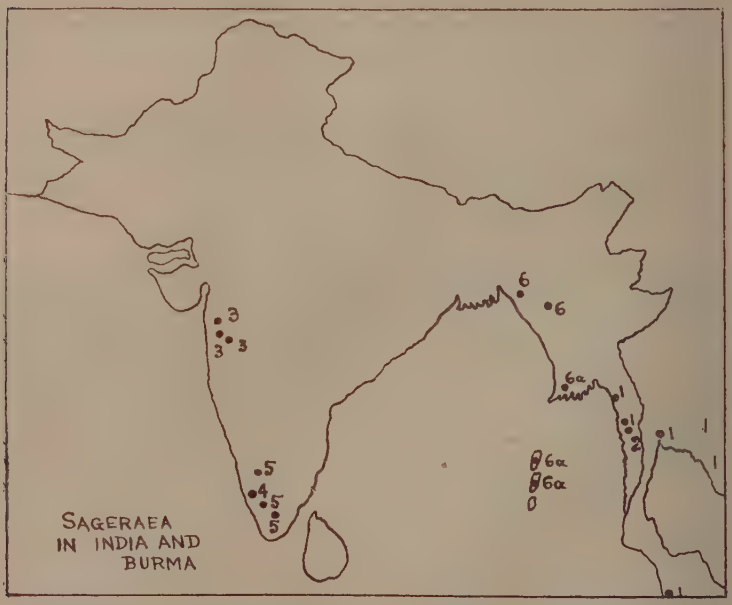
From the above it is clear that *Sageraea* has received different treatment from several taxonomists, and this appears to be due firstly to the fact that nobody has clearly differentiated the two genera by close comparisons and secondly to a superficial similarity.

In King's monograph on Annonaceae is perhaps the best account available of the present genus; but in his study two distinct species (*S. laurifolia* (Grah.) Blatter, and *S. Dalzellii* Bedd.) have been described as one under *S. laurina* Dalz. By uniting *S. Dalzellii* Bedd. with *S. laurifolia* (Grah.) Blatter, King maintained a confusion created by Hooker and Thomson in the 'Flora of British India,' which has been cleared up in the present paper and descriptions have been added of all the new species described in recent years.

Although *Sageraea* closely resembles *Bocagea*, it is not difficult to distinguish between them by certain distinctive characters. Thus :—

Character.	*Sageraea*.	*Bocagea*.
1. Aestivation of corolla.	Imbricate.	Valvate.
2. Anther cells.	Lateral.	Dorsal.
3. Ovules and seeds.	Many (rarely 1).	Few.
Type species.	*S. laurina* Dalz.	*B. multiflora* St.-Hil.

Sageraea is confined to South-East Asia, and the total number of Indian and Burmese species is six. These species have characteristically developed in the two humid regions as shown in the following map :—



Map showing the distribution of species of *Sageraea* in India and Burma. The numbers correspond to the numbers described in the present paper.

Sageraea Dalzell, in Hook. Journ. Bot. III, p. 207 (1851). *Bocagea* Hooker fil. & Thomson, in Hook. fil., Fl. Brit. Ind. I, p. 92 (1872). Glabrous elegant trees. *Leaves* alternate, entire shining. *Flowers* small, axillary or fascicled, often on woody tubercles on old branches, 1–2-sexual. *Sepals* 3, orbicular or ovate, usually imbricate. *Petals* 6, free, imbricate, usually biseriate, equal or unequal, concave. *Stamens* 6–28, in two or more series, thick ; anther-cells dorsal, oblong. *Carpels* 2 to 10 ; style very short or absent, usually capitate ; ovules 1–12 ; torus flat or convex. *Fruit* stalked and globose.

Key to the Species of Sageraea.

Flowers unisexual.
- Pedicels 6 mm. long ; petiole 4–6 mm. ; lamina 25–35 cm. long .... *elliptica.*
- Pedicels 25 mm. long ; petiole 8–12 mm. ; lamina 15–25 cm. long .. *bracteolata.*

Flowers bisexual.
- Flowers distinctly pedicelled (pedicels 1–3 cm. long), usually fascicled.
  - Stamens 12 ; inner petals larger than or almost equalling the outer series.
    - Lamina 10–20 cm. long ; pedicels 10–15 mm. long ..... *laurifolia.*
    - Lamina 25–35 cm. long ; pedicels 25–30 mm. long ..... *grandiflora.*
  - Stamens 25–28 ; inner petals smaller than the outer ..... *Dalzellii.*
- Flowers sessile or subsessile, usually solitary ..... *Listeri.*

Descriptions of the Species.

1. S. ELLIPTICA Hooker fil. & Thomson, Fl. Ind. p. 93 (1855) ; King, in Journ. As. Soc. Beng. LXI/2, p. 7 (1892), and in Ann. Roy. Bot. Gard. Calcutta, IV, p. 6 (1893) ; Brandis, Ind. Trees, p. 13 (1906) ; Finet & Gagnepain, Fl. Indo-Chine, I, p. 45 (1905) ; Ridley, Fl. Mal. Penins. I, p. 25 (1922) ; Craib. Fl. Siam. Enumeratio, I, p. 28 (1931). *S. Hookeri* Pierre, Fl. For. Cochinchine, t. 15 (1883). *Bocagea elliptica* Hooker fil. & Thomson in Hook. fil. Fl. Brit. Ind. I, p. 50 (1872) ; Kurz, For. Fl. Burma, I, p. 50 (1877). *Uvaria elliptica* A. DC. in Mém. Soc. Phys. et d'Hist. nat. Genève, V, p. 27 (1832) ; Wallich, Cat. nos. 6470 and 7421.

A large tree glabrous in all parts except the flowers. Branches stout, angled. *Leaves* large, shortly petioled, coriaceous, narrowly oblong, acute, margin entire and reflexed, base usually rounded, rarely cordate, shining above ; midrib raised below, grooved above ; lamina 20–35 cm. long, 4–9 cm. broad ; petiole thick, 4–6 mm. long. *Flowers* usually red, unisexual, solitary and axillary or fascicled on tubercles on the older branches ; pedicel 6 mm. long with several bracts near the base. *Sepals* 3, semi-orbicular, small, glabrous, ciliate at the margin. *Petals* 6, biseriate, thick, concave, ovate-orbicular, ciliate at the margin, 6 mm. long, inner smaller than the outer. *Stamens* 12–18 ; connective produced, quadrangular at the top ; anthers extrorse. *Carpels* 3, glabrous ; ovules about 8 ; ripe carpel subsessile, globose, glabrous, about 25 cm. in diam. Seeds several.

Distribution.—BURMA : Tavoy, *Wallich* 6470. Martaban, Doyookyee Pass, *Brandis* 925. Tavoy, Wagon, *Meebold* 16607. MALAYA : Penang, *Wallich* 4125 ; 7421. Malacca, *Maingay* 1587 A. SIAM : Kawchan, Lemdan, Panchibari, Chantaburi ; (*Craib*). COCHIN-CHINA : Cambodia.

2. S. BRACTEOLATA Parker in Ind. Forester, LV, p. 376, t. 15 (1929). A small tree, glabrous except for the inflorescence. Leaves 15–25 cm. long, 4·5–8 cm. broad, oblong, narrowed at both ends, thinly coriaceous ; midrib depressed above, prominent beneath ; main lateral nerves about 10 pairs, not conspicuous and not clearly differentiated from the intermediate nerves ; petiole 8–12 mm. long, rather stout. *Flowers* monoecious, both sexes similar in size and shape, red, in clusters on short woody tubercles from the branches below the leaves ; pedicels about 2·5 cm. long with small amplexicaul brown pubescent bracts at the base and a bracteole about the middle. *Sepals* 3 mm. long, coriaceous, rounded, ciliate. *Petals* very thick and fleshy, both series slightly imbricate, the outer 10 mm. long, broadly ovate, minutely ciliate, the inner smaller not ciliate.

Stamens 16, the outer larger than the inner ; connective slightly produced. *Carpels* 10, ellipsoid ; ovules 6–8 ; style 0, stigma capitate. Young fruits in clusters of 5 or 6, stalked, ovoid, 1 cm. in diam.

Local name.—Pa-ngan.

Flowers.—November ; *fruit*, January.

Distribution.—BURMA : Tavoy, evergreen forest near Kambok, *Parker* 2183, 7 November 1924 (type in Herb. Dehra Dun ; *cotype* in Herb. Maymyo). Thaungyin, Tadagyo, *Ba Pe* 13001 (Herb. Maymyo) in fruit. Mergui, Kampong Talok, Victoria Point, 300 m. *Su Koe* 6220 (Herb. Maymyo).

The wood is prized for making oars.

3. S. LAURIFOLIA (Grah.) Blatter in Journ. Bomb. Nat. Hist. Soc. p. 294 (1931). *S. laurina* Dalzell in Kew Journ. Bot. III, p. 207 (1851) ; Dalzell & Gibson, Bomb. Fl. p. 2 (1861) ; Hooker fil. & Thomson, Fl. Ind. p. 93 (1855) ; Baillon, Nat. Hist. pl. i, p. 96 (1871) : Beddome, Ic. Pl. Ind. p. 9 (1874) ; King in Ann. Roy. Bot. Gard. Calcutta, IV, p. 7, t. 35 B in part (1893) ; Talbot, For. Fl. Bomb. I, p. 33 in part (1909) ; Brandis, Ind. Trees, p. 13 (1911) ; Gamble, Ind. Timbers, p. 15 in part (1922). *Bocagea Dalzellii* Hooker fil. & Thomson in Hook. fil., Fl. Brit. Ind. I, p. 92 (1872) ; T. Cooke, Fl. Pres. Bomb. I, p. 17 in part (1903). *Guatteria laurifolia*, Graham Cat. Bomb. Pl. p. 4 (1839).

Medium sized elegant tree. *Leaves* alternate, oblong-lanceolate, coriaceous, shining above, dull beneath, apex subacute, base subcuneate or rounded, margin entire, usually reflexed ; midrib slightly raised below, grooved above near the base ; main nerves 10–14 pairs ; lamina 11–20 cm. long, 3–6·5 cm. broad ; petiole stout, 0·5–1 cm. *Flowers* bisexual, white, solitary or in small fascicles on minute tubercles appearing below the leaves, rarely axillary, 8 mm. in diam. ; pedicel 10–15 mm. long, slender with numerous scaly bracteoles at the base. *Sepals* 3, slightly connate at the base, imbricate, orbicular, thinly hairy. *Petals* 6, biseriate, thick and leathery, imbricate, orbicular, concave, 5–7 mm. long, subequal, glabrous, margin minutely hairy. *Stamens* 12, sessile, biseriate, outer row sometimes sterile and flattened ; connective broadly projecting, truncate ; anther cells linear, dehiscing longitudinally. *Carpels* 3–5, elliptic-ovate, glabrous, sessile ; stigma subsessile, capitate ; ovules 8–10 ; torus convex. Ripe carpels globose, glabrous, about 2·5 cm. in diam., subsessile, one-seeded. It is stated by some authors that the fruit contains four to six seeds, but the material examined by the author does not reveal more than one seed in each fruit.

Local name.—Sageree ; Sajeree ; Harkinjal ; Undie. The generic name has evidently been taken from Sageree.

Flowers.—October, November ; *fruit.*—January–February.

Distribution.—Endemic in Bombay Presidency on the western ghats : not found in Travancore as reported by Hooker, King and Talbot.

In the 'Flora of Assam' the authors have described this species as occurring in Assam under the name *S. laurina* Dalz. This seemed to the present author to be a highly interesting record of discontinuous distribution, and examination of the Assam material at the Herbarium of the Forest Botanist at Shillong proved that this record was a case of

misidentification. All the sheets labelled *S. laurina* Dalz. at the above Herbarium are incomplete specimens with fruits only, and probably do not belong to the genus *Sageraea*.

Distribution.—Bombay Presidency : Concan, *Stokes and Law*. North Canara, Ainshi, 650 m., *Talbot* 3158. Matheran, *Raoji* (Jan. 1893). Jwyar Hills, *W. Burns* (April 1909). Matheran, Kolaba, *H .P. Parenjpe* (Nov. 1907). Nagotna, *Graham*.

The species yields good timber ; wood red, hard, even-grained.

Note.—This species has long been confused with *S. Dalzellii* Bedd., although there exists a marked difference between the two species. King has overlooked this distinction in his monograph, and, following Hooker fil. & Thomson, has united *S. Dalzellii* Bedd. with the present species (usually known under the name *S. laurina* Dalz.). It was Brandis who first separated these two distinct species, and he was subsequently followed by Gamble in Fl. Pres. Madras (1915), 12.

For the sake of convenience the characters differentiating this species from *S. Dalzellii* Bedd. are shown below in the following table :—

	S. laurifolia (Grah.) Blatter.	*S. Dalzellii* Bedd.
Flowers	white	bright yellow.
Bracteoles	present	absent.
Stamens	12, outer row sometimes and flattened.	25–28, all fertile.
Ovary	glabrous	hairy.
Flowering season	October–November	March.
Distribution	Bombay	Malabar, Travancore.

4. S. grandiflora Dunn in Kew Bull. 1914, p. 182 ; Gamble, Fl. Pres. Madras, p. 12 (1915).

A large to medium sized elegant tree, all parts glabrous except the flowers. Bark wrinkled. *Leaves* oblong, shortly acuminate, entire, rounded at the base, pale above ; main nerves 10–12 pairs ; lamina 25–35 cm. long. *Sepals* 3, broad, ciliate, 2–3 mm. long. connate at the base. *Petals* 6, imbricate, rotundate, ciliate ; outer petals 1·5 cm. long, inner petals much larger. *Stamens* 12, obovate ; anther cells distant. *Carpels* 3, strigose ; stigma subsessile, entire ; ovules 12–14. *Fruit* unknown.

Travancore : Keni, evergreen forest 60–70 m., *Bourdillon* 469.

5. S. Dalzellii Beddome, Ic. Ind. Or. p. 9, t. 42 (1869, but dated 1874) ; and Fl. Sylv. Anal., Gen. t. 1 (1870) ; King in Ann. Roy. Bot. Gard. Calcutta, iv, p. 9, in part (1893).

A small evergreen tree with black bark ; branches slender and glabrous. *Leaves* shortly petioled, alternate, elliptic or elliptic-oblong, subacute or obtuse, rounded at the base, entire ; midrib raised below, grooved above all through ; main nerves 19–13 pairs ; lamina 20–35 cm. long, 8–11 cm. broad ; petiole stout, 10–13 mm. *Flowers* bisexual, bright yellow, 12 mm. in diam., in axillary fascicles of 4–8 flowers on woody tubercles on the older branches ; pedicel without bracteole, 3 cm. long. *Sepals* 3, rounded, cohering at the base, ciliate at the margin. *Petals* 6, biseriate, concave ; outer petals 6 mm. long, inner petals smaller. *Stamens* 25–28, all fertile, outer larger ; anther cells distinct. *Carpels* 3–5, oblong, hairy ; style distinct ; stigma capitate, entire ; ovules about 12 ; torus flat ; ripe carpels globose, stout.

Local names.—Moujanara ; Kanakaitha.

Flowers.—March ; *fruit.*—August–September.

Distribution.—S. India : Anamalai Forest ; Kerian Shola, 600–800 m. Malabar, Travancore, Tinnevelly.

Note.—There are three imperfect sheets with leaves and fruits only in Herb. Calcutta (*Calder and Ramaswami* 486, 486, and *Rama Rao* 1796) named *S. Thwaitesii* Hook. fil. & Thoms. These specimens do not agree in leaves and general appearance with the Ceylon *S. Thwaitesii* Hook. fil. & Thoms., especially in the fruits, which are surely too large for the latter. It is strongly suspected that these sheets represent either *S. Dalzellii* Bedd. or *S. grandiflora* Dunn. The fruit of neither of these species is known. The fruit of the present sheets is ovoid, hard, subsessile, 34–44 mm. in diam.

6. S. Listeri King in Ann. Roy. Bot. Gard. Calcutta, iv, p. 7 (1893).

A timber tree 30–50 m. high, attaining a girth of 2·5–3 m. in diam. at the base. Bark reddish brown and peeling off. Young branches slender pale, all parts glabrous except the flowers. *Leaves* shortly petioled, coriaceous, pale and shining above, elliptic to elliptic-oblong, shortly acuminate ; base cuneate or subcuneate, margin entire slightly reflexed, lower surface dark brown when dry ; main nerves 6–8 pairs, spreading, converging towards the margin, faint and indistinct on both surfaces ; midrib raised below ; lamina 10–16 cm. long, 3–7 cm. broad ; petiole 8–12 mm. long. *Flowers* hermaphrodite, silver-grey, subglobular, solitary, axillary or extra-axillary, sessile, 6 mm. in diam. ; bracts 1–3, basal, suborbicular, pubescent outside. *Sepals* much imbricate, very concave, orbicular, densely pubescent with minute yellowish grey hairs, glabrous inside, 3 mm. in diam. *Petals* 6, biseriate, more densely pubescent than the sepals, orbicular, inner row smaller than the outer, thick and concave. *Stamens* 9 ; connective broad, flattened, not produced at the apex ; anther cells lateral, extrorse. *Carpels* 6, free, ovoid ; ripe carpels broadly ovoid, glabrous but uneven, narrowed at the base, 2·5 cm. long, seeds about 12 in two rows, compressed. The original description of King states that the flowers are unisexual, but the examination of more complete material shows that the flowers are invariably bisexual and it is consequently necessary to modify the original description in this respect.

Local name.—Dhanian tree (Chittagong).

Flowers.—February–March ; *fruit.*—June–July.

Distribution.—Bengal : Chittagong Hill tracts, Barkal, *Lister* 120 (type in Herb. Kew ; co-type in Herb. Calc.), *Lister* 270. Coxbazar, *Heinig.* Mahallya, *S. K. Mukerjee* 121. Burma : Insein Distr. Pyinmadaw Reserve, *Parkinson* 34. Sandoway Distr., Sandoway Reserve, *Parkinson* 9719.

6 *a*. S. Listeri King var. andamanica Chatterjee et Mukerjee, var. nov. *S. Listeri* King similis, sed foliorum nervis approximatis 8–12 paribus, bracteis et staminibus numerosioribus, petalis longis exsertis, fructibus globosis, inter alia satis recedit.

Large tree, all parts glabrous except the flowers ; young branches slender ; bark rough and variously wrinkled. *Leaves* shortly petioled,

elliptic, entire, acuminate, base rounded or cuneate, margin reflexed below : midrib prominent on the lower surface, slightly grooved on the upper ; main nerves 8–12 pairs, distinct ; upper surface of leaf shining, lower reddish brown when dry ; lamina 10–17 cm. long, 3·5–7 cm. broad ; petiole stout, about 1 cm. long. *Flowers* bisexual, regular, minutely pedicelled, axillary, usually solitary, rarely occurring in pairs, ovoid or globular ; bracts many (10), semicircular or reniform, entire, thinly hairy, 2–4 mm. in diam., closely packed and imbricating, arranged spirally at the base of the flower and becoming lax as they approach the sepals. *Sepals* 3, broadly ovate, entire, acute, very much concave, thickened slightly at the base, 4 mm. in diam., densely tomentose outside with minute golden yellow hairs ; inner surface glabrous, faintly veined ; somewhat leathery. *Petals* 6, uniseriate, equal, strap-shaped, purple, glabrous on both surfaces, exserted from the calyx, 6 mm. long. *Stamens* 15, free, 2 mm. long ; connective hooded ; anther cells dorsal. *Carpels* 6, free, elliptic, slightly oblique, compressed on the inner side, glabrous ; style 0 ; stigma capitate, not very smooth, notched in the middle. Ripe carpels globose, smooth, 1·5 to 2 cm. in diam., one-seeded ; main stalk 5–7 mm. long, secondary stalk as long ; seed globose diam. 1 cm. slightly compressed on base and apex.

Local name.—Chai ; Chooi.

Flowers.—March–April ; *fruit.*—October–November.

Distribution.—Andaman Islands : *R.E.P.* Regd. No. 12585, March 1900 (*type* and *cotype* in Herb. Calc.). South Andaman, East coast, *R. L. Heinig* 322, 325, 375, November 1901 (fruit). Andaman, *Prain's collector* 304, 314, 339, November, 1900. South Andamans, Rutland, *C. Alfred* 828, July 1914. Burma : Bassein, Mezali Reserve, *Lace* 3008, 5 April, 1906 (in Herb. Kew, under *S. Listeri* King).

The variety yields good timber and is suitable for making planks. It is a large tree growing in the deciduous forests of the Andaman Islands and Burma.

Note.—This plant resembles the type of *S. Listeri* King sufficiently to have been long confused. It differs from the type in the number of leaf nerves, presence of more numerous reniform bracts at the base of the flowers, longer and exserted petals, and greater number of stamens.

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Summary.

The confusion between the American genus *Bocagea* and the Asiatic genus *Sageraea* is explained and the Indian and Burmese species of the latter are fully described and their nomenclature corrected. A new Andamanese and Burmese variety of *S. Listeri* King is recognized and described. An improved key to the species is also given.

OBITUARIES.

Mahbub Alam was born on 5 August 1901. He took his M.Sc. degree in Botany at the Lucknow University and thereafter did post-graduate training at the Imperial Agricultural Research Institute under the late Dr. F. J. F. Shaw, Imperial Economic Botanist. He was appointed as Assistant Economic Botanist, Bihar, in January 1929, and was promoted to the post of Economic Botanist from 1 April 1935. He was in charge of the Rice Research Station of the Imperial Council of Agricultural Research in Bihar from the inception of the scheme in January 1932, and in this capacity did very valuable work. He passed away on 26 February 1941. D. R. Sethi.

Dr. Rose Bracher, the elder daughter of Reuben Bracher, was born in 1894. After attending the school of which her father was headmaster, she went to Bristol University, where she graduated with First Class Honours in Botany in 1917. She spent a year in research under Professor O. V. Darbishire, took her M.Sc., and then acted as demonstrator for two years in the London School of Medicine for Women. As Rose Sidgwick Fellow, she spent a year at the University of Wisconsin studying Mycology and then went to London as lecturer at East London College. In 1924 she returned to Bristol as an investigator under the Department of Scientific and Industrial Research. In 1926 she was appointed Assistant Lecturer in the Department of Botany, in 1929 Lecturer, and in 1940 Senior Lecturer. This last title is given for distinguished service to the University. In 1927 she was awarded the Degree of Ph.D. A month before her sudden death on 15 July 1941, she had received the honour of being the first woman member of the non-professorial staff to be elected a member of Senate.

At Bristol Dr. Bracher applied and extended the methods of ecological survey she had learned with Professor Fritsch. She conducted a class every year with extensive excursions in the summer term. In the course of this teaching work she and her students accumulated much information on the vegetation of the Bristol district, and several valuable papers were published in the Proceedings of the Bristol Naturalists' Society and elsewhere. Her chief scientific work, however, was the investigation of the communities of Euglena on the tidal banks of the Avon, and especially the physiology of their striking periodic appearance and disappearance. The results of this work were published in three distinguished papers, the last of which appeared in the Journal of our Society. Two little books, ' Field Studies in Ecology ', and ' Ecology in Town and Classroom ', have proved extremely useful to teachers of biology. They include many of her own observations and methods.

Dr. Bracher was an admirable teacher, and she did a great deal of extra-mural lecturing. She had a large following, in Bristol and the neighbourhood, of working men and women whose interest in biology she had stimulated. In the University she acted as Warden of the Women Home Students' Society, a post in which she found scope for her close interest in the welfare of her students. She is greatly missed by a wide circle of friends both within and without the University. She was elected a Fellow of our Society in 1938. M. Skene.

Frederick Berry-Lewis Butler entered the Royal Botanic Gardens, Kew, as a student in June 1913. Before he had completed his botanical and horticultural studies, however, the Great War of 1914–18 broke out. He joined the army in December of that year, and served in the Royal Army Medical Corps until the end of the war. On being released from the Army he returned to Kew and was selected for the post of Botanical Field Assistant in the Department of Agriculture, Kenya Colony. He proceeded to Kenya, and served in the above capacity until 1922, when it was decided to stimulate an increase in the agricultural exports of the colony by a closer co-operation with the native population, and he was chosen to help in this work. In his new post as Agricultural Superintendent he spent most of his time touring the districts under his charge, advising and helping the chiefs and peasants in the cultivation of their crops. Particular attention was paid to crops suitable for export, such as cotton and maize, and besides the planting and cultivation it was necessary also to supervise the marketing and grading of the crops. As the exports of this and other produce including coffee and oil-seeds increased, it was necessary to take steps to maintain a high standard of produce in order to preserve the colony's good name on the export markets. Grading and storing regulations were brought into force for this purpose, and Butler was selected for this new work as a Grader and Inspector of Agricultural Produce. In the ensuing years he applied himself with great zeal to his work and carried it out with such success that he was promoted to the post of Chief Grader and Inspector of Produce, Cyprus, where he arrived to take up his new duties, on transfer from Kenya Colony, at the end of January 1935. In his new sphere his work was largely concerned with the maintenance of high quality in the citrus fruit and potatoes exported from Cyprus, and to this was added the control of adulteration. The volume of work was considerable and required close co-operation with the Customs Department. Always keenly interested in his work, Butler kept himself so fully occupied with his official duties that, apart from departmental reports, he found little time for recording the botanical work in which he was always interested but found so little time to indulge.

He died in Cyprus on 9 August 1941. He had been a Fellow of the Society for almost twenty years. J. D. Snowden.

Lady Busk (1861–1941).—Marian, afterwards Lady Busk, was the younger daughter of Lewis Balfour, silk merchant. She studied Botany and Chemistry, both privately, and also at Queen's College, London, where she matriculated in June 1879, 15th in Honours; passed the Intermediate Science in 1881 and obtained the degree of B.Sc. in 1883, being among the first women to do so. A few years later she returned to the College to take the first course in Advanced Botany to be organized, 'having a knowledge of plants' as her teacher recorded 'beyond that of the ordinary student, adding a certain distinction to that small and exceptionally brilliant class'. Subsequently, in conjunction with Miss Mary F. Ewart, afterwards Mrs. Macdonald, she assisted Professor Oliver with the translation of Kerner's 'Natural History of Plants' which was published in 1894. She was elected a Fellow of the Linnean

Society on 5 April, 1905, being among the earliest women Fellows. She took an active interest in the Women's Suffrage movement and was at one time Hon. Treasurer of the University of London Graduate Women's Suffrage Society.

She married in 1880 Edward Henry, only son of Henry William and Mary Anne Busk, an eminent teacher of Law and conspicuous educationalist, knighted in 1901. L. Balfour.

Robert Henry Corstorphine was born at Arbroath on 13 November 1874 and died there, after a few weeks' illness, on 25 March 1942. He was the only son of Henry Corstorphine, who for many years was English Master at Arbroath High School. Here the son received his early education, proceeding afterwards to the University of St. Andrews, where he obtained the degree of B.Sc. While Botany was to become his main recreation during a long and active business career, it may be recalled that after taking his degree, he was engaged for a few years in the teaching of Chemistry, first at the Technical College, Glasgow, and subsequently at Dundee. Teaching did not remain his profession for long, however, and Corstorphine returned to Arbroath to take over the management of a firm of printers and publishers. For nearly forty years he acted as managing director of the firm and was closely associated with *The Arbroath Guide*, the first number of which appeared in 1842. His keen personal interest and his knowledge of Botany were largely responsible for the publishing by his firm in recent years of a number of botanical books and scientific periodicals.

Corstorphine's interest in natural history was aroused when he was a student at St. Andrews, and he never lost his youthful zest and enthusiasm for the study of plant and animal life. He had a great affection for all dumb creatures. A day's fishing or a game of golf provided occasional recreation, but his greatest outdoor interest lay in the exploration of his native county of Angus: the glens and hills of Clova made a twofold appeal to one who was both botanist and mountaineer. His knowledge of the flora of Angus was unequalled—though he was exceedingly modest about it—but he was always ready to share his knowledge and experience with others.

For thirty years Corstorphine worked on the flora of Angus, checking old records and gathering new data with a view to the publication of a county Flora which would replace Gardiner's *Flora of Forfarshire*, now nearly a hundred years old. In his field work and in the formation of a magnificent herbarium of Angus plants, he had the constant help and encouragement of his wife, also a keen and able botanist. It was hoped that the new Flora would be ready for publication soon, and those who knew something of the work which Corstorphine had put into its preparation knew also that it would be worthy of a county already famous through the botanical journeys of George Don. It has been intimated that the herbarium is to be housed at University College, Dundee, and there is good reason to believe that a *Flora of Angus*, based on Corstorphine's work, will eventually be completed—a fitting tribute to one whom British Botany could ill afford to lose. J. R. Matthews.

Captain DOLLMAN, who died on 21 March 1942, was known to a wide circle of Fellows of the Linnean Society, not only as a frequent and welcome speaker at our scientific meetings but as the exhibitor of many interesting and effectively displayed specimens of mammals at our soirées.

John Guy Dollman, born on 4 September 1886, was the elder of the two sons of J. C. Dollman, R.W.S., the distinguished painter, best remembered perhaps for his picture, 'A very gallant gentleman', a tribute to the memory of the heroic Captain Oates. This picture is now the property of the Cavalry Club. The father's interest in natural history, transmitted to his sons, is evident in the careful studies of animals introduced with dramatic effect in many of his pictures.

Guy Dollman and his brother Hereward were together at St. Paul's School, where they were early marked out by their scientific and artistic ability. Both won the Smee prize for natural history, and both were repeatedly successful in the John Watson prize competitions in the art department. Together with some others of similar tastes they started the school natural history society and museum which have continued to flourish ever since. In their boyhood also the brothers began making their own collections of British beetles, moths and butterflies, collections which were later to become sufficiently important to be desirable accessions when they were presented to the Entomological Department of the Natural History Museum. Hereward died in early manhood of sleeping sickness, contracted while serving as entomologist in investigations on that dreaded disease for the British South Africa Company.

Guy went up to Cambridge in 1905 with a scholarship from St. Paul's and an exhibition from St. John's College. He read for the Natural Sciences Tripos, but it may be conjectured that he found some of the teaching in zoology little to his taste, especially in the prevalent disparagement of systematics. In the beginning of 1907 he applied for and obtained an appointment in the mammal section of the Zoology Department of the British Museum (Natural History). From then until he graduated in 1908 he was allowed to travel daily between Cambridge and London in order to keep his terms.

For some years after entering the museum Dollman was mainly occupied with the routine work of determining, registering and incorporating accessions to the collection and occasionally describing new species and subspecies of mammals. In course of time he came to devote his attention specially to the Ungulata, Carnivora and Primates.

Early in 1915 he volunteered for military service and enlisted in the Inns of Court O.T.C. In due course he was commissioned in the 19th London regiment. He was soon promoted to Captain and appointed a Divisional Bombing Officer. Later he commanded a bombing school in the 2nd London reserve Brigade. He was severely injured in a bombing accident which permanently impaired the sight of one eye, but he returned to duty and served till the end of the war as Brigade Bombing Officer in the Southern and Eastern Commands.

On returning to the Museum Dollman took over the arrangement of the exhibition galleries of mammals, of which the late Mr. Richard Lydekker had been in charge, and soon began the preparation of the

' habitat group ' of African elephants in one of the alcoves of the central hall. Here at length he found work for which his artistic abilities specially fitted him. Such habitat groups, in which animals are shown in their natural surroundings, had been developed with much elaboration and at vast expense in some of the larger American museums, but until then nothing of the sort had been attempted on a large scale in the British Museum. The elephants, male, female and young, belonged to the nearly extinct Cape race of the African elephant, now surviving only in the Knysna Forest, and were presented by the Government of South Africa. The scene represented was on the borders of the Knysna forest and the background was painted by Dollman from photographs of the spot. The tree-trunks, brushwood and dried foliage were specially collected by the Cape Forestry Department, while many of the plants were modelled in various materials and painted in Kew Gardens with the assistance of Mrs. Dollman. The amount of work involved in the designing and preparation of such an exhibit is perhaps not to be guessed at by those who have not watched it growing from day to day.

The elephant group attracted the admiration of many visitors from royalty downwards, and it was planned to follow it by others, especially by a group of Gorillas, for which preparations were made over a period of years. Mr. Reginald Akroyd, F.L.S., undertook, at his own expense, an expedition to the Birunga mountains to obtain specimens and photographs of the characteristic vegetation of the Gorilla country. But the financial depression had set in and no money was available, and, further, the discovery of suitable places for such exhibits in a building designed for quite other purposes proved a matter of great difficulty, so the Gorilla group never developed beyond a rather charming small-scale model in plasticine which stood in one of the galleries for some years.

Unexpectedly, however, the financial crisis was to provide Dollman with another opportunity to display his talents. The spacious and handsome new Whale Hall had just been completed and no funds could be provided for the costly task of mounting the huge skeletons and casts which it was to contain. We were debating what use could be made of it when Dollman came to me with the suggestion of a temporary exhibition of the larger Mammals under the title of ' Game Animals of the Empire '. For this purpose the specimens were borrowed from the cases in the mammal galleries and grouped on the floor of the hall on a ground of peat litter which suggested, without attempting to imitate, their natural surroundings. The exhibition, referred to by ' The Times ' as ' a still-life Whipsnade ', proved to be extremely popular with visitors. As some of us had expected, the geographical arrangement proved much more to the taste of the layman than a zoological classification would have been. The fact that the animals were not enclosed in glass cases, combined with Dollman's skilful and artistic grouping, gave them a vividness and solidity that surprised even those most familiar with them. Altogether the experiment was very successful and made us wonder whether some of our traditional ideas on the arrangement of museum galleries should not be revised.

By this time Dollman was widely recognized as an authority on the larger mammals. At the International Conference for the preservation

of the Fauna and Flora of Africa which met in London in 1933, he was one of the panel of scientific advisers and was largely responsible for drawing up the schedule of animals which the Conference recommended for partial or total protection.

Dollman wrote many systematic papers on mammals and was also the author of the ' Catalogue of the Selous collection ', and the ' Guide to the Horse ' and other guides issued by the Museum. He also wrote ' The Game Animals of Africa ', ' The Game Animals of India ', and three editions of Rowland Ward's ' Records of Big Game '. He contributed numerous popular articles to magazines (including the ' Natural History Magazine ' formerly published by the Museum), and was a very acceptable lecturer and broadcaster on natural history topics.

Dollman's interest in art was second only to his enthusiasm for natural history. He was an accomplished painter, and his pictures were frequently hung at the Royal Academy and other important exhibitions. He was for many years secretary of the Civil Service Arts Association and was responsible for organizing their annual exhibitions.

In 1916 Dollman married Violet, younger daughter of the late Dr. S. F. Holloway, and I am indebted to her for many of the facts recorded in this notice. His brother, on the same day, married her sister who, only a few months later, died from sunstroke in Central Africa.

I found Dollman invariably a most friendly and helpful colleague. He will be greatly missed in the Museum. W. T. Calman.

Robert John Flintoff (1873–1941) was of Quaker stock, and was born at Lower Broughton, Salford, Lancashire, on 15 August 1873. His ancestors had Yorkshire associations. A member of one of the oldest and most respected Quaker families which has been associated with the City of Manchester for three generations, he ever retained a deep affection for his old school and college here. His great-grandfather came to the cotton city from Guisborough, Yorkshire, and became a prominent Mancunian and Chairman of the Royal Exchange.

The future naturalist was educated at the Manchester Grammar School and studied Chemistry at Owens College. He then became associated with the firm of F. Scott & Co., Calico Printers, Littleborough, where he became chemist and eventually a partner. On retirement in 1909, he followed in his great-grandfather's footsteps and resided for a time at Haxby, near York. He then removed to Bridlington, and eventually settled at Goathland. The open air and the countryside ever had a strong appeal for him, and prior to coming to Goathland he was a keen oarsman, equestrian, and huntsman, and also took an active interest in yachting.

It was about 1924 that our friend succumbed to the charms of the delectable North Yorkshire uplands and acquired Water Ark Lodge, Goathland, overlooking the moors. This commodious and pleasantly situated residence is situate in a veritable naturalists' paradise. To the west lies the extensive moorland parish of Danby-in-Cleveland, ' one of the widest and wildest parishes of England ', where lived and laboured that singularly devoted incumbent, John Christopher Atkinson (1814–1900), whose intense love of natural history, the open air, his fellow men,

folk-lore and antiquities found congenial scope. The writings of this worthy successor to Gilbert White and his notable book, ' Forty Years in a Moorland Parish ', will need no introduction to many and afford a valuable record.

Flintoff was intimately attuned to his new environment and though nominally in retirement, the last twenty years or so of his life were in reality a strenuous period. His wonderful gardens brought much joy and pride and absorbed considerable practical attention for a time, though apiculture and horticulture were later left largely in the hands of others when his natural history pursuits made increasing demands on time and energy. A valuable and extensive library was much used and typical of its owner. Its well-filled shelves were rich in select works on natural history, topography and antiquities, whilst English literature, classics and religion also found due representation. Here we recall his affection for English and the classics. He had an excellent memory in this connection and could recite from Shakespeare at considerable length.

His affection for the countryside was deep and enduring and embraced the people, folk-lore, fauna and flora.

That large natural amphitheatre the picturesque and impressive Hole of Horcum, which lies below the road near Saltersgate between Pickering and Whitby, was only a few miles from his home. This had a great attraction for him and he visited it annually for more than twenty years, sometimes on several occasions yearly, making careful notes and observations relating to its natural history. He also interested others in the subject, and one result is seen in the published papers and contributions for which he was directly or indirectly responsible. His observations and researches brought him into touch with many naturalists and scientific authorities. He was a voluminous, tireless, and at times an embarrassingly frequent correspondent.

Flowering plants, birds and other vertebrates made special appeal to him, and problems of adaptation and variation always aroused his interest. It was a result of such predilections that he founded, financed and practically arranged the affairs of The Northern Ecological Association in 1936. This aimed at stimulating ecological work in relatively small areas. It was felt that careful local work, continued year after year, over sufficient periods would produce valuable result. The study of individual species was encouraged as also individual effort in the team spirit. Care was taken to avoid some of the disadvantages attendant on certain societies and unions. This Association soon consisted of over 400 members, for its aims and objects had wide appeal. The work entailed was very considerable for he was practically single-handed and without clerical help, but he dealt with this with his usual energy and optimism.

' He harnessed a remarkable team of scientific workers, ranging from eminent University professors to gardeners and gamekeepers—a truly democratic combination—in the worth-while task of studying life-forms as directly conditioned by native environment '. The success was most gratifying and membership ranged over the length and breadth of Britain, and local branches were formed by groups of zealous workers.

He was able to persuade his colleagues to prepare monographs on various aspects of the subject and treated them generously in various

ways. Thus reprints and illustrations were often provided, and in some cases a worker not too well circumstanced was gifted with an honorarium. Space precludes adequate reference to his generous and lovable character and his hatred of insincerity and sham.

Water Ark Lodge was a place of pilgrimage for many, for our hospitable friend was ever delighted to receive and entertain kindred spirits. Amongst his wide circle of friends were the late Canon R. Fisher, J. F. Robinson of Hull (author of 'The Flora of the East Riding'), Dr. G. C. Druce, H. J. Wilkinson (the York botanist), and particularly James Green, game-keeper and naturalist of Thornton Dale.

He wrote, 'Try and strive to do Right for Right's sake . . . All else you will learn in the fulness of time, and meanwhile be honest, be kind, be cheerful'. His life and activities provided many illustrations of the practical exemplification of his faith and ideals. Thus, he founded and fostered The Friends' Club, Goathland. Membership was limited to men of the parish who had served in the last war. Meetings of an undenominational nature were held on Sunday afternoons and an annual dinner was arranged.

His published work is represented by a considerable total of natural history contributions, and he was a most diligent member of the Editorial Board of 'The North Western Naturalist'. He did much to call attention to the natural treasures of the British countryside, and his efforts for his beloved Goathland district recall those of Canon Atkinson in his neighbouring area. A Fellow of this Society from 1932, he was also a Fellow of the Chemical and Zoological Societies.

His end came suddenly and unexpectedly. On 13 September he went for a walk to a favourite haunt, the tiny and beautiful hamlet of Beck Hole, a spot dear to the Nature lover and the haunt of many interesting forms of life. He collapsed as he was returning and never recovered consciousness when taken home, and the call came the same evening.

'The North Western Naturalist' for December contains some biographical account which has been utilized in the present tribute. This also contains an excellent portrait of our friend in his garden. He is standing by a sun-dial on which he had recently inscribed 'Robert J. Flintoff, F.L.S.' and the words of Omar :—

> 'Yon rising Moon that looks for us again—
> How oft hereafter will she wax and wane ;
> How oft hereafter rising look for us
> Through this same Garden—and for *one* in vain !'

After cremation the ashes were strewn over his beloved garden. His high ideals and special interests were reflected in his disposition of a not inconsiderable estate. Substantial endowments were willed ultimately to pass to the Linnean Society (for a medal for botanical research), the Chemical Society (for a medal for the most meritorious contribution to the knowledge of the relations between chemistry and botany), and to the University of Manchester (for a prize for post-graduate students doing research work of outstanding merit). His old school was not forgotten, and, in addition to a contribution to the new building fund of Manchester Grammar School, he left an endowment for a prize for the

scholar showing the best knowledge of one of Shakespeare's plays. His library, pictures, natural history journals and notebooks were also willed to the School. Subject to a life interest, the residue of the estate was left on trust for Manchester Grammar School for founding scholarships and in defraying the cost of publication of his articles on research.

A. A. Dallman and T. Sheppard.

Benjamin Millard Griffiths was born at Kidderminster in 1887. He entered the University of Birmingham in 1905, and took the B.Sc. Degree of that University in 1908; the D.Sc. Degree was conferred on him in 1923. Towards the end of the war of 1914–18 he was appointed assistant to Prof. Yapp at Belfast, and in April 1920 lecturer in Botany at Reading. He held the latter position only for one term, since in the following October he was appointed lecturer at Newcastle. In 1924 he became reader in charge of the new botanical laboratory, established at Durham, and remained in that post until the end of his scientific career. He died on 25 March 1942.

His early scientific work, carried out in conjunction with G. S. West, dealt with the giant bacteria of the genus *Hillhousia*, but most of his scientific papers related to the Algae and to limnology. During the last twenty years of his life he was mainly occupied with investigations of the plankton of the lowland pools of Great Britain. A general paper dealing with these themes was published in the 'Journal of Ecology' in 1923. In this an attempt was made to correlate the occurrence of certain planktonic Algae with some of the factors of the environment. Griffiths realized that 'any attempt to classify lakes and pools in terms of their plankton constituents is impracticable', but that 'a classification of the plankton Algae in terms of their relationship to the ecological features prevalent in the pool is quite possible'. A considerable number of investigations, dealing with individual pools or groups of pools, appeared in the 'Journal of the Linnean Society' and in the 'Journal of Ecology' during subsequent years, in some of which a more detailed consideration of the factors was undertaken and data were furnished covering one or more annual cycles. Griffiths' work showed considerable promise, and it was no doubt the breakdown of his health during the later years of his life that reduced his output of scientific work and prevented its attaining full fruition. He was also an active collector of the seeds of wild and cultivated plants, but I am not aware that he ever published anything about them.

Griffiths played a part in the foundation of the Freshwater Biological Association and for a number of years represented the University of Durham on its Council.

F. E. Fritsch.

Arthur Grove.—By the death of Arthur Grove on 2 February 1942, the Society has lost an ardent horticulturist, a great writer on horticultural subjects, and, above all, an authority on the genus *Lilium*, and the doyen of lily cultivation in this country.

Though an engineer by profession, Grove was early attracted to gardening, and, coming under the spell of H. J. Elwes' enthusiasm, he became also interested in Systematic Botany. He was elected a Fellow of the

Society in 1903, and though not a regular attendant at the Meetings he was well acquainted with its activities and had a warm regard for its welfare.

Arthur Stanley Grove was born in 1865 and was the youngest son of Sir George Grove, the editor of 'The Dictionary of Music and Musicians', and first Director of the Royal College of Music. His second christian name commemmorated his maternal uncle, Dean Stanley. He was educated at Marlborough, and was afterwards trained in electrical engineering. He enjoyed his work and for many years practised in his chosen profession.

His gardening career started at Kentons, near Henley, where he gradually assembled a collection of rare and interesting plants. He tried anything he fancied, though the chalky nature of the soil decidedly restricted his activities. But knowing most of the good gardens in the country his interest in plants was always wide. He had a great eye for beauty, both of colour and of form, and he knew all that was best amongst garden plants. It was at Kentons also that he began his collection of lilies. He had wonderful successes but equally inexplicable failures. There can be no doubt that many of the latter were due to the presence of Virus diseases, which in those days were completely unknown. He attributed his failures to unfavourable soil, but more often to Botrytis, a fact which sometimes led him in his writings to over-emphasize the importance of this parasite.

It was in 1905 that Grove published a small volume entitled 'Lilies', which sold well. He soon became a recognized authority and developed and maintained a very large and world-wide correspondence. For many years he industriously collected material for a comprehensive volume. This, however, never took shape.

In 1930 he agreed to prepare the text for a 'Supplement' to Elwes' great work 'A Monograph of the Genus Lilium', to be brought out in Parts by Dame Alice Godman. This he did voluntarily out of regard and admiration for his old friend. The work was to be accompanied by hand-coloured plates prepared from exquisite originals by Miss Lilian Snelling.

The species described in the first two Parts were fairly straightforward, but the history of many of the other species was long and complicated and the nomenclature involved. Partly through ill-health and partly owing to these taxonomic difficulties Grove sought, after the second Part was issued, professional assistance, and eventually joint authorship with the present writer was agreed upon. Though we did not always see eye to eye we worked perfectly harmoniously together, and the memory of that association is one I shall always cherish. Grove's intimate knowledge of lilies in gardens was invaluable, but his vast accumulation of notes and cuttings were not without sundry red herrings which for him sometimes obscured the issue and served to impede progress. It was with considerable relief that the last Part was published and distributed to subscribers early in 1940, before air raids commenced. As it was, part of the stock was lost when the premises of the publishers were destroyed.

Grove's literary work must be emphasized. He wrote well and easily, and often with great charm. For many years he contributed to 'The

Times', and he also wrote numerous signed and unsigned articles for 'The Gardeners' Chronicle', 'Country Life', and other journals. He always wrote the weekly gardening article in 'The Times' himself, and by his pen he served and influenced horticulture in a variety of ways. He was awarded the Victoria Medal of Honour in Horticulture of the R.H.S. in 1924, the Veitch Memorial Gold Medal in 1934, and the Gold Medal of the Massachusetts Horticultural Society in 1936. He was, moreover, the first recipient of the Lyttel Lily Cup.

During his last few years Grove lived at Kew, and though his strength failed he greatly enjoyed carrying out experiments and working in his garden, where he had collected a variety of rare and choice plants such as could seldom before have existed in so small an area within 8 miles of Charing Cross. He will always be remembered for his whimsical humour and charm of manner and for his great love of beauty in plants.

A. D. Cotton.

Patrick Martin Hall who died at Fareham, Hampshire, on 5 August 1941, was born 14 March 1894. He was a Scholar of Winchester College from 1907 to 1913, and a Scholar of Oriel College, Oxford. During the 1914–1918 war he saw service in Mesopotamia, gaining a staff appointment; in the present war he was engaged in very arduous work in connection with food-control in several southern counties.

Though actively engaged in business as a Chartered Surveyor and Land Agent, in the firm of Hall, Pain and Foster, Portsmouth, he found time to do a considerable amount of botanical work; joining the Botanical Society and Exchange Club of the British Isles, in 1914, he became Honorary Editor in 1936. Hall specialized in the study of the *Nominium* section of *Viola*, in *Orchis* and *Utricularia*, was referee for the families of these genera for the club, and was to have been contributor for them in the new Students' British Flora. He was elected a Fellow of the Linnean Society in 1934.

He had a keenly critical mind and his well-balanced judgment was equally pronounced in field and herbarium. His cheerful outlook on life and vivid enthusiasm made him an ideal companion on botanical expeditions, and there are many who will miss his ever ready help and friendship.

N. Douglas Simpson.

Sir Arthur William Hill (1875–1941); University Demonstrator in Botany, Cambridge, 1899; Fellow of King's College, Cambridge, 1901; University Lecturer in Botany, 1904; Assistant Director, Royal Botanic Gardens, Kew, 1907; Sc.D. Cantab., 1919; F.R.S., 1920; Director of the Royal Botanic Gardens, 1922; C.M.G., 1926; President of Section K, British Association, 1930; K.C.M.G., 1931.

Arthur William Hill was the younger of the two surviving children of Daniel Hill, of Herga, Watford. In the large garden of his father he took his first lessons in plant-life. Then he was sent to school at Marlborough, a delicate lad, and for that reason a day-scholar under the care of an aunt who resided in the town. It may have been that the resultant measure of isolation led him away from the playing fields to the open country; at any rate, on the downs he took his second course of lessons in plant-life.

Edward Meyrick, the entomologist and one of his masters, encouraged his botanizings and that he should aim at a scholarship in Cambridge : so it was that he competed in 1893 in a college-group examination, and was selected for an exhibition at King's, later to become a Scholar. He took the highest honours in the Natural Sciences Tripos (1897 and 1898) and followed these successes by post-graduate research under Sir Albert Seward, ' On the structure and affinities of a Lepidodendroid stem ' (Trans. Roy. Soc. Edinb. xxxix, pp. 907–31 ; 1901).

Hill's interest, however, was keener in directions other than fossil botany. He had become very skilled in microscopic technique—was indeed very proud of his ability to make pretty sections—and it flattered him greatly when Walter Gardiner, who had the same skill, invited his collaboration, put into his way a grant from the Royal Society, and gave him working room in his own private laboratory. This event dominated his scientific research from 1898 to 1907, i.e., through his years of teaching in Cambridge, and quite properly when the advanced courses were distributed among the teachers Histology was assigned to him. He had been University Demonstrator in Botany from 1899 to 1904 when he became University Lecturer.

The research in Gardiner's laboratory resulted in the following publications :—' The distribution and character of connecting threads in the tissues of *Pinus sylvestris* (Phil. Trans. Roy. Soc. Lond. B 194, pp. 83–125, 1901, a joint paper), ' The histology of sieve-tubes in *Pinus* ' (Ann. Bot. xv, pp. 575–611 ; 1901) : ' The histology of the endosperm during germination in *Tamus communis* and *Galium tricorne* ' (Proc. Cambr. Phil. Soc. xi, pp. 445–54 ; 1902) ' and ' The histology of the sieve-tubes in Angiosperms ' (Ann. Bot. xxii, pp. 246–90 ; 1908). The titles accurately convey the scope.

During the years of teaching he took opportunities of joining two expeditions. The first was to Iceland with William Bisiker (1900), in whose book ' Across Iceland ' (1902), is a list by Hill of his gatherings of larger plants. Except *Ophioglossum vulgatum* he had been unable to add to the known flora of the parts he passed through ; but he collected Algae from hot springs, and among them G. S. West found material of greater interest (Journ. Bot., 1902, pp. 241–8). The second expedition was to the Bolivian Andes. Leaving Liverpool on 30 October 1901, he joined a travelling companion at the Falkland Islands, passed through the Straits of Magellan and up the west coast of South America to Mollendo, where the health of his companion failed. Thence he went forward by himself, circled Lake Titicaca and came back by the same way. His experiences in the Andes covered the first three months of the year—their late summer and autumn. There are two accounts of this journey, one in the Report for 1904 of the Marlborough College Natural History Society, and the other in the ' Scottish Geographical Magazine ' for May 1907. The experiences were to lead him from histology into ontogenetic and taxonomic research. He had met with species of the curious Umbelliferous genera, *Lilaeopsis* (syn. Crantzia) and *Azorella*, and he read a paper on them to the Cambridge Philosophical Society (abstract in Proc. xii, part v, 1904). The hillsides over Lake Titicaca were dotted with cushions (Azorella-like in form), conspicuous and attractive, of various Malvaceae

which at the time was all classified under *Malvastrum*. Hill was intrigued by these and, after bringing his collections home, went into their systematy, and divided them between *Nototriche* and *Malvastrum*, monographing the former (Trans. Linn. Soc. Lond., Bot. ser. 2, VII, pp. 201–66; 1909) and the arborescent species of the latter (Journ. Linn. Soc. Lond., Bot. XXXIX, pp. 216–30; 1909). A third interest, and on the whole the most fruitful one, was found in the peculiar unequal cotyledons of tuberous species of *Peperomia*. On these he wrote 'The morphology and seedling structure of the geophilous species of *Peperomia*, together with some views on the origin of the Monocotyledons' (Ann. Bot. XX, pp. 395–427; 1906) and 'A revision of the geophilous species of Peperomia with some additional notes on their morphology and seedling structure (Ann. Bot. XXI, pp. 137–60; 1907). Later in life he returned to Lilaeopsis to monograph it; and he never ceased from gathering additional information on the Malvaceous genera.

The first papers on curious cotyledons were followed at intervals by a series, all in the 'Annals of Botany'—'The origin of the Monocotyledons' (XXII, pp. 713–4; 1906); 'Studies in seed-germination—the genus Marah' (XXX, pp. 215–22; 1916); 'Studies in seed-germination—Experiments with Cyclamen' (XXXIV, pp. 417–29; 1920); 'Typhonodorum Lindleyanum, the development of the embryo and germination of the seed' (XLIII, pp. 437–50; 1929, jointly with L. A. Boodle), and 'The Monocotylous seedlings of certain Dicotyledons with special reference to the Gesneraceae' (N.S. II, pp. 127–44, 1938); and akin to these were the papers 'The method of germination of seeds enclosed in a stony endocarp' (XLVII, pp. 873–87; 1933, and N.S. I, pp. 239–56; 1937). What may be said by way of summary on these contributions to our knowledge of seedlings?—The papers are stepping stones; but towards the end something bridge-like began to appear when Hill drew them partly into one view by dislodging a facile interpretation of monocotyly in Dicotyledons as due to union of the two cotyledons. His experiments on Cyclamen had been ingenious.

Hill appreciated and rightly used for this work on seedlings his extremely favourable position at Kew, where there was horticultural skill to help him and an unusual richness in material. He used this same position again for an interesting late paper which did not have its roots in his Andine journey, namely his 'Resupination studies of flowers and leaves' (Ann. Bot. N.S. III, pp. 871–87; 1939)—a good quarry. I wonder if he had thoughts of reminding ontogenists of a very legitimate use of the plant-wealth at Kew.

Reverting to Lilaeopsis, which I have mentioned as a first fruit of his Andine travel, its interesting distribution in the World caused him to study in turn the southern species of the genus *Caltha* (Ann. Bot. XXXII, pp. 421–35; 1918) and then to monograph *Lilaeopsis* (Journ. Linn. Soc. Lond., Bot. XLVII, pp. 525–51; 1927), and to follow these by 'Antarctica and problems of geographical distribution' read to the International Congress of plant-sciences at Ithaca in 1926 (Proc. II, pp. 1477–86), wherein he said:—'That there was a large and extensive land mass which we may call Antarctica seems certain . . . and it seems equally certain that from this last continent, which enjoyed from time to time a temperate or even

a subtropical climate, plants were distributed to South America . . ., Australia and New Zealand '. Botanists have reason to get down to the discussion on the suggestion in this place of repetition in climatic changes.

A visit to Australia and New Zealand in 1927, acted as a refresher to his interest and was followed by notes on the southern dispersal of *Cocos* (' Nature' of 27 July and 5 October 1929).

Professor T. F. Brooks has narrated (Obit. Notices, Roy. Soc. for 1941), the manner of Hill's selection in 1907 for the post of Assistant Director at Kew, and Sir Thomas Middleton, then Professor of Agriculture at Cambridge, has indicated (' Nature ' of 22 November 1941, p. 622) Hill's reaction to the offer. A great change it made in his scientific life. He had commenced taxonomic work by the side of his histological researches. The latter he now laid aside entirely, as well as his teaching : he never even returned to his University as an examiner, but gave himself up entirely to tasks belonging to his new post. Among these tasks was the editing of the ' Kew Bulletin ', for which he wrote signed and unsigned articles. There is only one way now in which the identification of his authorship of unsigned articles is possible, namely, in a personal file which he kept. He undertook, conjointly with Sir David Prain, the elaboration of the Gentianaceae for the ' Flora Capensis ' (VI/1, pp. 1036–1121 ; 1909), and revised J. G. Baker's account of the Santalaceae for the ' Flora of Tropical Africa ' (VI/1, pp. 411–34; 1910) and elaborated the latter family for the ' Flora Capensis ' (V/1, pp. 135–212; 1915)—an exacting piece of work. In the course of his studies of the Gentianaceae he discovered the curious organization of the stigmas of *Sebaea* in two tiers (Ann. Bot. XXVII, pp. 480–9 ; 1913), as had Rudolph Marloth about the same time. A revision of the genus *Strychnos* as it occurs in the East becoming due, he undertook it (Kew Bull. 1917, pp. 121–210). These taxonomic studies, like those on Malvaceae, started earlier, were put out with finished technique.

During the War of 1914–18 the Government used him in the planning of the vast cemeteries in France and Italy, where lie so many brave British.

In 1922 he succeeded Sir David Prain as Director of the Royal Botanic Gardens. Never was appointment more inevitable : Hill and Kew had become identified. Thenceforward to measure Hill's administrative success, measure Kew's success. He was favoured by the growth of ideas of unity in the Empire, and shared them, took advantage of them, and was singularly favoured in having T. F. Chipp as his Assistant Director until 1931. I was astonished at their success in developing co-operation on a great scale. It was done with the aid of much travelling, in which both took part, but eventually Hill only. Hill's two earlier and purely botanical expeditions have been mentioned : later he took opportunities of leave to visit various parts of Europe. In 1910 he went officially to Algeria, with the opportunity of a little botanical exploration, and in 1912 he paid his first visit to the West Indies on the same terms. After he became Director he went on Empire business successively to the West Indies, Australia and New Zealand, Java, Malaya and Ceylon, Sweden, West and South Africa, North America, South and East Africa, and India. Comment has been made that he became one of the most

travelled of botanists—botanist, yes, and much travelled also ; but it is only just to Botany to distinguish between journeys where personnel is the object and journeys where plants are the object. The former leave 'hazy first impressions' of the flora and do not make 'a travelled botanist' such as was Sir Joseph Hooker. However, Hill never over-exploited his knowledge of this nature.

At home, Hill, with the unrivalled opportunities of Kew, though with little leisure, added to his studies what he could and, considering the calls on his time, did much, as well as keeping his mind on a variety of the aspects of his science. Using Kew, he made investigations into the origins of some cultivated plants, Primulas, for instance (Journ. Genet. II, pp. 1–12 : 1912, and VII, pp. 193–8; 1918), and Pelargoniums (Journ. Roy. Hort. Soc. LXIV, pp. 353 and 358; 1939), and he was able to direct his staff toward work he desired done. He was generous in co-authorship, even to placing the names of quite junior subordinates before his in the titles of papers written. His greatest services to Botany must be counted administrative, and chiefly in imperial partnership. His approach to colonial development I find instructively given in his 'Report on matters of botanical interest in New Zealand' (N.Z. Journ. Sci. & Technol. X, pp. 53–9 : 1928). Ask where you will and the reply comes that his advice was rated high.

He left his diaries of travel to Kew. They are very full memoranda. He told the writer that he intended to edit them before he handed them over ; but he never found the time to do so. However, there is little in them personal enough towards others for removal. They record the doings of each day, and in the earlier diaries the record always begins with a statement how he had slept. Banter on this Pepysian touch he would not have understood, for he had even less than most men the power of facing himself in another's mirror. Was the touch a relic of the delicacy of his constitution when a child ? The inability made for both strength and isolation.

He worked his staff in open order.

His artistic judgement was excellent and, acting on it, he did much for the embellishment of Kew. He had a keen delight in a beautiful flower, and was exactly in the right place in the many services which the Royal Horticultural Society obtained from him. The Society repaid by giving him in 1934 the Victoria Medal of Honour, and in 1936 the Veitch Memorial Medal. He had a like delight in the beauty of a horse, and expressed it by riding, though he was an indifferent horseman. He liked order as he liked beauty, and above all things his office and personal library were in the strictest order. He was generous and careful at the same time ; and few knew the extent of his generosity, for it was very quietly bestowed.

On the morning of Monday, 3 November 1941, he went for a solitary ride. No one saw the accident by which he met his death. It is probable that his horse stumbled ; at any rate he went over its head, dragging the bridle off, and was killed by his fall.

At the time of his death he was engaged in writing a paper on certain aspects of the history of Kew. It is unfortunate that he was unable to complete this as he had studied the subject very carefully.

In 1924 he persuaded the Forestry Commission to find land for a plantation of Conifers such as will not grow at Kew. This plantation, which is at Bedgebury, near Tonbridge, and is doing well, is more peculiarly a monument to his name, because it is more exclusively his, than other services he did in continuation and perfection of changes passed on by those he succeeded.

He never married, and his sister who shortly predeceased him, dispensed for him the hospitality of the Director's house at Kew.

I. H. Burkill.

Mr. J. W. Haigh Johnson was essentially a man of the West Riding of Yorkshire. He received his early scientific training in the nineties at the Yorkshire College, Leeds, and after a short period of service in the laboratory of a public analyst he joined the Chemical Staff of the West Riding of Yorkshire Rivers Board, in 1897 or 1898, and remained in the service of the Board until a few years ago, when he retired.

Mr. Haigh Johnson's association with the late Professor West, whose daughter he married, encouraged him to develop and extend his knowledge of the biological sciences, and these he applied in his studies of the biology of water and sewage. Just over twenty years ago, the West Riding of Yorkshire Rivers Board established a Biological Department in its laboratories, and Mr. Haigh Johnson was transferred from the Chemical Department of the laboratories to take charge of the new Biological Department. He rapidly became a recognized authority on the biology of water and sewage, and his contributions to this subject in the scientific journals and in special reports to the Rivers Board break a good deal of new ground.

Mr. Haigh Johnson was a Bachelor of Science of Victoria University, Master of Science of Leeds University, and a Fellow of the Institute of Chemistry and of the Linnean Society.

He is survived by his wife, who, as already stated, was the daughter of the late Professor West, and by one daughter. H. T. Calvert.

Arthur Francis George Kerr was born at Kinlough, Co. Leitrim, on 7 February 1877. He was educated at Dorchester Grammar School—his parents having moved to Dorset—and afterwards at Trinity College, Dublin. There he took a degree in botany (B.A., 1st Senior Moderatorship), and in 1901 his medical degrees (M.B., B.Ch.). A year later he went to Siam as assistant to Dr. Campbell Highet, and when in 1903 the latter became Medical Officer of Health to the City of Bangkok, Kerr went north as Medical Officer of Health in Chiengmai.

On his first leave home in 1908, Trinity College granted him his M.D., 'for his gifts to the College Gardens'. When war broke out in 1914, Kerr came to England and joined the R.A.M.C., serving with it as Temporary Captain until 1918.

His love of botany began in boyhood, but it was not until he went to northern Siam that it became the engrossing work of his life. Outside his medical work he devoted all his time to the study of the flora of the country. He had a wonderful field before him, for botanically the country was almost unknown.

In 1920 he was appointed Director of the Botanical Section of the Ministry of Commerce of Siam, and from that time gave up his medical work. He planned then to make a botanical survey of the whole country, collecting everything that came his way regardless of whether it had economic value or not, and so to build up a herbarium for future workers in the country. It was a big undertaking, for Siam is a large country, and to complete it in the years at his disposal meant hard work. Only those who accompanied him on his tours have any idea of the amazing energy of the man. He would march all day and then sit up half the night preparing his specimens and writing up his notes upon them ; at dawn the next day he was up and ready to start again. Although he travelled fast, he seldom seemed to miss anything. He was wonderfully observant in spite of the fact that he was almost colour-blind. He was indifferent to the hardships and discomforts that attend all travelling in the interior of Siam, where roads and rest-houses are non-existent and food often difficult to procure.

His survey was completed in 1933, the last tour being one to NE. Siam and French Laos. As well as field work, Kerr was occupied with administrative work, the organization of his department and the arrangement of his vast herbarium. After his retirement from Siam he went to Indo-China for some months.

Kerr was one of the most generous of men. He gave freely of his time, and often also his money, to help scientific workers. He gave his life to Botany without thought of reward or distinction from it. Although he had an unrivalled knowledge of the flora of Siam, he refused to describe the many new species that he collected, for he was a meticulous worker, and felt that without full material for comparison and books for reference, such as could be found only in a great museum, it was better to leave that side of his work to others.

For many years he sent all his material to Professor W. G. Craib for description, and when Craib was asked to compile the ' Enumeratio Florae Siamensis ' he gave him his full support. Nevertheless, he published many articles concerning his tours in Siam and the observations he had made upon plants at different times. When Craib died, in 1933, Kerr was appointed to continue the Enumeratio. The work is now about half completed, but there is no one with the knowledge of the Siamese flora to succeed Kerr.

Of orchids he was particularly fond, and in addition to the large collection that he accumulated, he made sketches of them from life. On the medical side of botany he did much work on *Hydnocarpus* and the Chaulmugra oils in regard to the treatment of leprosy.

His herbarium, after supplying the country in which he worked so long, is divided between the Royal Botanic Gardens, Kew, and the British Museum (Natural History). His collection of sketches and his photographs of plants are at Kew.

Kerr married Daisy Muriel Judd, in 1903 ; she died in Siam of malignant malaria. Three daughters survive him. MALCOLM A. SMITH.

C. C. A. MONRO.—Those who knew Monro respected him as a scientist, and liked him as a man whose great personal charm was combined with

considerable culture and wide interests. Although I intend to dwell mainly on his scientific work, other aspects of his complex personality must not be omitted.

Charles Carmichael Arthur Monro, born on 14 September 1894, in India, was the youngest son of Alexander Monro, Director of Public Instruction, Central Provinces. Three generations of his ancestors, all bearing the name Alexander, were Professors of Anatomy in Edinburgh University, and the second (1733–1817) gave his name to the ' Foramen Monroi ', connecting the third ventriculus of the brain with the first and second. When showing me the portraits of these distinguished members of his family, Monro suggested that he probably inherited his interest in biological sciences from them. His family also produced the well-known Homeric scholar, David Binning Monro (1836–1905), Provost of Oriel College, Oxford, who might also have influenced Monro's interest in classical literature and Latin, to the study of which he originally intended to devote his life.

Monro was educated at Charterhouse, Eton, and Trinity College, Oxford. At Oxford he took Pass Moderations in Classics in 1914, and began to read for the Honour School of Literae Humaniores. He was a man of wide reading and had a great love and understanding of poetry and literature. He was opposed to narrow specialization, arguing that it may absorb all other intellectual interests, and I remember him once saying that to be an expert in worms one must know Shakespeare.

The course of Monro's life would have been quite different had not his University years been interrupted by the Great War. He served in Belgium and France and was wounded in 1916. It was probably during this period that he became interested in Biology, for on his return to Oxford in 1920 he began to read until 1922 for the Honours School of Natural Science. His decision to study Biology was probably also influenced by his intense desire to comprehend the problems of life, and this may explain his great interest in metaphysical and neo-scholastic philosophy. In his thirties Monro became an ardent Catholic, and his religious faith had a great influence on the remainder of his life. He was keenly interested in the relations between science and religion, and in 1939 delivered a lecture on this subject at a Summer School at Cambridge. In his views and ways of thinking, however, Monro was far from conventional. In intellectual discussions he always displayed great originality, and valued this quality in other people. He once told me that he regretted the small number of people in England who would devote their lives to proving that the earth was flat, or is the centre of the Universe. We must regret that his premature death prevented him from formulating his thoughts so that they could become known to a far wider circle than those who knew him personally.

From November 1922, when Monro was appointed an Assistant Keeper in the Department of Zoology, British Museum (Natural History), he concentrated his attention on the Polychaete worms, but his intense energy urged him to undertake additional activities. He continued to maintain his interest in philosophy, literature and art. He was also keenly interested in foreign politics, and for a time held the position of Honorary Secretary of the Catholic Council for International Relations.

Soon after the outbreak of war, feeling that his scientific work was non-essential in wartime, Monro offered his services to the Ministry of Food. His services were accepted, and he remained at the Ministry until his death, which followed an operation, on 21 June 1942. Since 1939, when he left the British Museum, Monro's wartime occupations did not allow him any spare time for research work.

Monro wrote the greater part of the 'General Guide to the Exhibition Galleries', published by the Museum in 1931, and the 'Instructions for Collectors, No. 12—Worms' (1932). He also edited a series of postcards dealing with the old herbal 'Hortus Sanitatis', to which he was able to apply his rare knowledge of medieval Latin, acquired during his early studies before the Great War. He wrote the chapter on Worms in Pycraft's 'Standard Natural History' (1931), and contributed several articles, signed C.C.A.M., to the 14th edition of the 'Encyclopaedia Britannica'. The most important of these are:—'Annelida' (excluding the section of Oligochaeta, written by J. Stephenson) (vol. I): 'Echiuroidea' (vol. VII), and 'Sipunculoidea' (vol. XX). From 1925 to 1927, Monro was editing the Museums Journal, and one of his last works was the preparation and editing of a new 'Collector's Handbook', containing instructions for the collection and preservation of invertebrates, undertaken by him jointly with Dr. H. A. Baylis, the author of an obituary of Monro published in 'Nature' (vol. CL, p. 84; 1942).

His main attention, however, was devoted to the study of Polychaeta, and he has written a number of systematic memoirs which are an important contribution to the subject.

In his Oxford days, Monro did not specialize in any particular group, and became interested in Polychaeta only when he was placed in charge of the collection of Annelids and Echinoderms in the British Museum. Although he had a great love and understanding of nature, he was not a field zoologist, and was not particularly interested in the study of the native fauna. Having free access to the large Museum collections and literature, he soon gained a prominent position among the leading authorities on the Polychaeta, and, thanks to his great personal abilities, he quickly developed the qualities required in a good systematist. Although Monro maintained a considerable interest in general zoological problems, and did not fail to record any ecological or zoogeographical observations, his work was almost entirely devoted to the study of preserved material. He regarded his duties in the Museum as primarily to make a quick and accurate determination of material, and this he did unfailingly. He has since won the name of the 'perfect systematist' in a short obituary note published in 'Nature' (vol. CL, p. 85; 1942), by Professor T. A. Stephenson, to whom he gave assistance in ecological work carried out during the Barrier Reef Expedition and during an ecological survey of the South African Marine Fauna.

In his study of Polychaeta, Monro was the follower and great admirer of Prof. P. Fauvel, whom he regarded as the leading authority of his group.

In 1924, he published his first paper in a series dealing with the material collected by H.M.S. *Alert*, mainly off the coast of Queensland, in the China Sea and in the Magellan Region. In 1928, he started another

series of seven papers on the material collected by Dr. C. Crossland, and Dr. Th. Mortensen, thus making an extensive contribution to our knowledge of the Polychaeta on both Pacific and Atlantic sides of Panama. The results of his study confirmed Professor Fauvel's contention that among the Polychaeta of those regions the tropical fauna includes many species common to the Atlantic, the Pacific and the Indian Oceans.

In 1931, Monro published his first paper on brackish-water Polychaeta, describing a new species, *Nereis meggitti*, collected in a tidal zone on the shore of Rangoon River, and thereafter he never lost interest in rare cases of adaptation of Polychaeta to life in brackish and fresh waters and the changes which it effects on the structure of the body of worms. In the case of *Nereis meggitti*, certain features of the structure led Monro to the opinion that we have here the vestige of the complete heteronereid changes undergone in the past by the species while it lived in the sea, and that whereas the complete epitocous transformation no longer occurs, owing to the adoption of a river habitat, traces of it remain in the partial modification of the feet at the time of sexual maturity.

The most valuable of Monro's works is his memoir on the Antarctic Polychaeta of the *Discovery* Expedition, to the study of which he devoted many years of hard work. Another valuable contribution was the paper of the B.A.N.Z. Antarctic Expedition of 1929–31 (1939). Out of 122 species taken from Antarctic and sub-Antarctic waters, 105, or 86 per cent, were known from both the eastern and the western ends of the Antarctic Continent, and may therefore be regarded as circumpolar.

Being chiefly engaged in systematic research, Monro did not miss any opportunity of dealing with other problems. Thus he described the post-larval stage in *Diopatra cuprea* Bosc (1924), published a note on the pelagic phase of a Terebellid worm (1931), and wrote a short paper on incubation and parental care in marine worms (1928).

Although Polychaeta were the main object of Monro's study, he possessed a considerable knowledge of Echinodermata, Hirudinea and Echiuroidea.

The list of Monro's publications, 41 in number, in itself provides a good account of his work, interrupted by his premature death. It can be consulted at the British Museum (Natural History). L. Cernosvitov.

Charles Arnold Newman was born in Barnsley, Yorkshire, in 1872, his father being a partner in the firm of Newman and Co., solicitors. He was educated at Shrewsbury School and Trinity College, Cambridge. He was prevented by a legal technicality from taking his brother's place in the family firm, and went to Messrs. Upperton, solicitors, of Lincoln's Inn Fields.

He married Kate Beck, of Loughborough, and his two elder sons were born while he lived in London, but in 1904 he retired and went to live in Oundle. His main interests were developed here. He was always an omnivorous reader, a habit to which his deafness contributed, he having been deaf from an early age, and becoming gradually more so as time went on. His reading consisted mainly of English literature, of which he had a very wide knowledge and a highly developed taste ; but he was particularly interested in history, especially the social history of the

nineteenth century. In later life he became a profound student of the Gospel of St. John. Soon after he came to Oundle he was put on to the notion of microscopy by a chance conversation in the train, and this became a constant occupation. He was a skilled handler of a microscope, and his main fields were the green Algae, Polyzoa and Rotifers of fresh water. He was a good general biologist, although his education had been purely classical, and having been brought up in the generation influenced by Huxley, he had a lasting interest in the theory of evolution.

His house was to him a constant joy, and in its decoration he largely followed William Morris (whom he had known), though with a personal taste and application which were highly characteristic. He knew a good deal about both domestic and ecclesiastical architecture.

Deafness prevented his taking any part in local or national politics, but he never allowed it to interfere with his social activities. There can have been few men whose company was more continually sought, especially by the young, for whom he had an understanding and over whom he exercised an enormous influence. He was associated with many institutions which brought men together, especially those which united men of all kinds. He became a Freemason in 1911 and was a member of many Lodges and of many Degrees. He became Prov. Gd. S.W. Later, he became increasingly interested in Toc H activities.

At the beginning of the last war, being too old for military service, he went to work in a shell factory in Sheffield. The giving up of his home life, the society of his wife, and the upbringing of his children were to him a greater sacrifice than to most. The physical discomfort counted for much less than the penalty of living in lodgings. He started work as a labourer with a wheelbarrow, but rose to the charge of the Department of Steel Testing. His universal popularity with the roughest lot of men (and women) ever gathered together was a source of great pride to him.

After the war his income was much reduced, and he sold the large house in Oundle and rented a house in Cotterstock, two miles away. He bought the house ultimately, which was a good thing, because it gave him the opportunity of again having a house of his own, to decorate as he liked. The proper education of his children involved considerable sacrifice, but his tastes were simple and money, as such, meant nothing to him. His only expenses were on books, of which he collected first and finely printed editions, and wine and cigars, for both of which he had a cultivated palate.

Although he looked his age, he kept his zest for life unimpaired, and so far from restricting his interests, he added to them constantly. Indeed, his interest in glass was added to that for china during the post-war years, as were many new literary enthusiasms—for Trollope's novels, for example. He was like Samuel Pepys (for whom he had a considerable admiration) in his capacity for interest in almost anybody and anything. It would be easier to make a list of those things for which he had no enthusiasm than of those in which he was interested.

His influence on others probably sprang in no small measure from his humility : he seemed to take it for granted that anybody, even his own children, knew just as much as he did on the topic under discussion, and that their opinions were as likely to be of value as his own. He

never entered a room without everyone realizing that somebody who mattered had come in, and talk always sprang into activity in his company, without his apparently taking any particular part in it.

He was almost quixotically generous, and it was characteristic of him that he gave away largely during his life, but did not leave a penny to charity, in the belief that his money was his own to do as he liked with while he was alive, but that leaving to charity was only an underhand method of robbing his heirs.

His physical disability to take any active part in this war was a great distress to him, and the strain of sitting at home in a village, with nothing to do but worry over the newspaper was the worst possible preparation for a serious illness. It probably contributed more to his death than materialists would recognize.

He left a widow and three sons, Dr. Charles Newman, Sub-Dean of the British Postgraduate Medical School, Dr. James Newman, Deputy Medical Officer of Health to Warwick, and Commander Rudolf Newman, R.N., in the Engineering branch of the Service. CHARLES NEWMAN.

A great English naturalist, CHARLES OLDHAM, was born in Lincoln 16 April 1868, and died at his home, Oxfield, Berkhamsted, Herts., 13 April 1942, within three days of completing his seventy-fourth year. He was a fine figure of an Englishman, over six feet in height, thin and sinewy, a great walker and climber, with strikingly handsome features and expressive kindly eyes, which won the confidence of all men and women and especially of children and dogs. He kept to the old fashion of wearing a beard, and when out walking always wore spectacles and carried a telescope.

In the words of Prof. Edward J. Salisbury (' Nature ', 2 May 1942, vol. CXLIX, p. 496) Oldham's ' loss to science is the greater because in these days of " learning more and more about less and less ", the number of those who combine the insight of the specialist with a balanced perspective is growing fewer although the need for them increases '.

The salient facts of Oldham's career can be stated briefly. When he was about six years old his family left Lincoln and went to live at Sale, Cheshire, as his father had business as a merchant in Manchester. The young Charles was educated first at a preparatory school at Sale, and then at Manchester Grammar School. At the age of sixteen he commenced work in an insurance office in Manchester, was later transferred to London and became an assistant manager of the Commercial Union Assurance Company. After living for some years in Watford, he moved to Berkhamsted, where he called his house, in Shrubland's Road, ' The Bollin ', from happy memories of the Cheshire river. Six days a week he went to London and back by train.

In 1927 he retired on pension, and a few years later had built for himself a new house, Oxfield, in a remarkably beautiful garden of his own design, with a dew-pond, on the ridge of high land, known as Shootersway, which extends from above Berkhamsted to near Wigginton above Tring, Here he was able to give his whole time to his nature studies, and his energy to assisting the many scientific societies in which he was so keenly interested and which he helped, not only from his knowledge of natural

history, but especially, as a member of committees and sub-committees, from his acquaintance with business matters and official practice in drafting rules and bye-laws.

In 1907 Oldham joined the Zoological Society of London, and also the British Ornithologists' Union and Club : he served on the Union's Committee 1926–9, and, as Vice-President, 1936–8. In 1913 he was elected a Fellow of the Linnean Society, and in 1936 became a member of Council. He always took interest in the progress of the Manchester Museum, and among the societies of which he was an active member were the Conchological, Freshwater Biological, Malacological, Ray and, especially, the Hertfordshire Natural History.

He married, first in 1895, Fanny Tyas, daughter of S. A. Tyas, of Sale, who died in 1900 ; and second in 1930, Dorothy, the widow of his brother Roger, and daughter of Charles Scorer, of Lincoln. We tender our sympathy to Mrs. Oldham, who survives him, and to his sister Miss May Oldham.

The predominating features of Oldham's character were his love of truth and his devotion to the ideal of doing all he could in every way to help his fellow men.

He had a profound interest in and knowledge of the British Isles, their geology, scenery, geography, history, botany, zoology, languages, dialects, place-names, folk-lore, general literature and poetry. Every well-reasoned movement for the protection and preservation of British scenery, plants and animals had his warm support. His conversation was always of fascinating interest ; he had a very keen sense of humour and an apparently inexhaustible fund of really amusing anecdotes and stories, always brought in at appropriate moments and always told quietly, and briefly, in as few words as were necessary.

During his school and business days at Manchester, Oldham became very interested in the fauna and flora of Cheshire and Lancashire, but managed to spend holidays with relations and friends in his native Lincolnshire and in Cambridgeshire.

Oldham loved all England, Wales, Scotland and Ireland, but, it appeared to me, his heart-strings were most strongly tied to those parts of East Anglia which are between Norwich and Lincoln. He delighted to explore every small island round the British coasts, even to distant Foula, and, where there were inhabitants, there Oldham made, and kept, friends.

During recent years he visited Switzerland more than once to enquire into, and finally elucidate, an important question in the distribution of European land-snails. He also made a pilgrimage to Uppsala for the special purpose of examining some type-specimens of Mollusca.

The dates of publication of Oldham's scientific writings extend to over half a century, from at least 1890 to 1941. A full list of these, we are told, has been prepared for printing by the Hertfordshire Natural History Society.

The majority of Oldham's papers were concise, valuable notes on some particular subject ; his larger contributions to ornithology appeared in collaboration with his old school friend Thomas Alfred Coward, who died in 1933, and in the standard volumes of Harry Forbes Witherby.

STANLEY S. FLOWER.

William Plane Pycraft, who was elected an Associate of the Linnean Society in 1898 and a Fellow in 1923, died on 1 May 1942, at the age of 74 years. He was born at Great Yarmouth close to the Norfolk Broads, where the wild life attracted him early to the study of natural history. His devotion to the subject led him to adopt it as his career, and on leaving school he went as a private pupil to Mr. Montagu Browne, Curator of the Leicester Museum, where he learned the art of preparing and preserving animals for study and exhibition. I met him first in 1891 at the house of Mr. Browne in Leicester, and in the following year I introduced him to Professor (afterwards Sir) E. Ray Lankester, who was looking for an assistant to help him to make zoological preparations for the Oxford University Museum. Mr. Pycraft then removed to Oxford, and while occupied with his routine work had the opportunity of attending Professor Lankester's lectures and demonstrations, which gave him a wide knowledge of the anatomy and classification of animals. In 1898, when Professor Lankester was appointed Director of the British Museum (Natural History), Mr. Pycraft accompanied him to London as temporary assistant. A few years later he joined the staff of the Zoological Department of the Museum, and remained there in charge of avian and mammalian osteology until his retirement in 1933, when he removed to the country, near Chertsey, Surrey, to resume the field observations which had stimulated him in his youth.

His chief studies were always in ornithology, and in 1905 he published his first original paper in 'The Ibis' on the feathers of the Tinamous. Three years later he presented to the Linnean Society an elaborate memoir on the feathers of the Owls, which was printed in the seventh volume of the Society's 'Transactions', 1898. In 1900 he described and discussed the feathers of the Megapodes in Dr. Arthur Willey's Zoological Results of an expedition between 1895-7, confirming the opinion that these birds are related to the Gallinae. In the same year he published another large memoir on the Morphology and Phylogeny of the Palaeognathae (Ratitae and Crypturi) and Neognathae (Carinatae), in the 'Transactions of the Zoological Society', vol. xv, emphasizing the very close relationship between the Struthious birds and the Tinamous. The palate of these birds was further discussed in the 'Journal of the Linnean Society, Zoology', vol. xxvii, in 1901. In this research he was specially aided by the Hon. Walter (afterwards Lord) Rothschild. Between 1898 and 1907, while he was arranging the skeletons in the British Museum (Natural History) he contributed a series of nine valuable papers on the osteology of birds to the 'Proceedings of the Zoological Society'. At the same time he prepared a useful 'History of Birds', which appeared in 1910, and in later years he collected materials for a volume on 'The Birds of Great Britain', which was published in 1934.

In 1915 Mr. Pycraft was entrusted with the study of some human skulls collected by the Wollaston Expedition to New Guinea, and henceforth he was much interested in human craniology. He began by realizing the unsatisfactory character of the Frankfurt Base-line, which was then generally used in the descriptions of human skulls. He pointed out that as it involved the variable upper part of the face as well as the cranium, it gave a false impression of relationships. He therefore proposed a new

base-line extending from the nasion to the auricular meatus, which allowed the cranium to be studied and described independently. He adopted this base-line in his report on the skulls from New Guinea and also in a later description of the fossil Boskop skull from South Africa. In 1928 he contributed to a volume on the fossil Rhodesian skull which was published by the British Museum. He inferred from a pelvis and leg bones found in the same deposit as the Rhodesian skull, that the Rhodesian man walked with a stooping gait and outwardly bent knees, and might therefore be referred to a distinct genus, which he named *Cyphanthropus*. He was also inclined to agree with those who had proposed to regard several of the existing races of man as forming distinct species of the genus *Homo*.

Throughout his career Mr. Pycraft endeavoured to stimulate public interest in the study of natural history, and he wrote several volumes which are not merely compilations, but include some results of his own researches. Among these may be specially mentioned his works on ' The Infancy of Animals ', ' The Courtship of Animals ', 1913, and ' Camouflage in Nature ', 1925. His small ' Stories of Bird Life ', ' Fish Life ', and ' Reptile Life ', published by Newnes between 1900 and 1905, are also noteworthy. His weekly article on natural history in ' The Illustrated London News ', which he contributed for many years, until his last illness, was a special feature of this paper, and attracted wide attention.

A. Smith Woodward.

Harry Joseph Riddelsdell entered business after school but, studying in his spare time, took the B.A. degree of London and gained an exhibition at Jesus College, Oxford, where he graduated in honours and won the Hall-Houghton Senior Greek Testament prize. He took Holy Orders and became one of the curates of Leeds parish church. For seventeen years from 1897 he was Sub-Warden of St. Michael's College, first at Aberdare and later, when the College moved, at Llandaff. In 1914 he was appointed Rector of Wigginton, and after the Great War became Vicar of Bloxham ; he was also rural dean of Deddington and examining chaplain to two successive bishops of Monmouth. He retired from parish work in 1936 and three years later a stroke put an end to all work. He died on 17 October 1941.

His interest in botany was roused while he was still at Oxford, and his long residence in the rich and unworked field of South Wales enabled him to gain an extensive knowledge of the flora. From 1901 onwards he contributed to the ' Journal of Botany ' numerous field notes and records and occasional critical papers, and in 1907 ' A Flora of Glamorgan '. He was a copious collector, and sent regularly to the Botanical Exchange Club a large parcel with many useful notes.

Under the guidance of the Rev. W. Moyle Rogers he made a special subject of the difficult and critical genus *Rubus*, and visited many parts of Great Britain to study the brambles *in situ*. When Rogers died, his books and manuscripts, with an invaluable selection from his *Rubus* specimens, came into Riddelsdell's hands. With these aids he determined specimens for collectors and extended his own knowledge. The more important conclusions reached by Rogers were printed in the ' Journal

of Botany ', 1920–1, and in 1930 the distribution records of *Rubus* according to Rogers' and Riddelsdell's determinations were brought up to date. From 1921 he worked at the genus in collaboration with the present writer, and a number of new forms were described.

The work, however, to which he gave most of his leisure and thought was the ' Flora of Gloucestershire ', sponsored by the Cotteswold Naturalists' Field Club. He accepted the editorship in 1908, and thenceforth spent much time and labour in dealing with the mass of records and lists already accumulated and in reorganizing and directing the work of the Club members. In the ' Proceedings ' of the Club, he issued many reports on the Flora and articles on matters of local botanical interest as well as (in 1933) our joint paper on ' Some *Rubus* problems in the light of Genevier's herbarium '. After his retirement in 1936 his time and energies were devoted to the completion of the Flora and a final revision had made some progress when illness compelled him to leave the task unfinished.

With Riddeldell his vocation always came first ; he was a scholarly and faithful servant of the church, personally devout and unworldly and beloved by all who knew him. From early years he made full use of leisure and considerable intellectual gifts, allowing no difficulties or discomforts to interfere with his purpose. His happy and appreciative temperament, his energy and enthusiasm, his quick eye and manifold interests made him a delightful companion in the field and in the study.

He was elected Associate of the Linnean Society of London in 1925. His herbarium includes a large collection of *Rubus* from many parts of Great Britain and many *Hieracia* from Wales ; incorporated with that of the present writer it is preserved in the British Museum (Natural History) at South Kensington. W. C. Barton.

John Joseph Sheldon died on 14 February 1942 at the ripe age of 84. After his retirement from business in 1923, he devoted the greater part of his time to his large garden. His interests were preponderatingly horticultural, rather than botanical, but he was an expert on varieties of British ferns, of which he had a large collection. He was an assiduous hunter of wild varieties of ferns, his tough constitution and power of concentration enabling him to search in suitable localities for many hours on end. In his garden he raised a large number of varieties by sowing spores. Mr. Sheldon was a Vice-President of the British Pteridological Society and was Treasurer of the Society for many years. On grounds of advancing years, he resigned the Treasurership in 1938, and his activities later became sadly impaired. His calm disposition and friendly nature endeared him to all who knew him. P. Greenfield.

Charles Davies Sherborn, who was elected an Associate of the Linnean Society in 1912, was the son of a well-known artist, Charles William Sherborn, who designed and engraved book-plates. He was born in Chelsea on 30 June 1861, and died in Fulham on 21 June 1942, having spent all his life in London. On leaving school he entered business for a short time, but he was more interested in natural science, and he soon decided to follow a scientific career. Having then received a small

legacy, he studied for a year in the University of Strasburg. In Chelsea he attracted the attention of his neighbour, Professor T. Rupert Jones, who enlisted his help in completing the two monographs on the Tertiary Entomostraca and on the Crag Foraminifera, for the Palaeontographical Society. Sherborn thus acquired a good knowledge of the shells of Entomostraca and Foraminifera as studied by geologists, but he became impressed with the difficulty of finding all previous references to the subject. He therefore began to devote special attention to bibliography, and in 1888 he published ' A Bibliography of the Foraminifera ', which was followed in 1896 by ' An Index to the Genera and Species of Foraminifera '. He also joined Arthur Smith Woodward in preparing a Catalogue of British Fossil Vertebrata, which was published in 1890. At that time Dr. B. Daydon Jackson was actively engaged on his great work the ' Index Kewensis ', which collected all the names of genera and species of flowering plants proposed since the time of Linnaeus. Sherborn formed the idea of preparing a similar index to the names of genera and species of animals recent and fossil, and henceforth he made an' Index Animalium ' his chief life's work. He was encouraged in his undertaking by the Trustees of the British Museum, who gave him all facilities for his bibliographical researches and eventually appointed him a temporary assistant in the Museum. His first volume, comprising 65,000 names proposed between 1758 and 1800, was published in 1902 by the Cambridge University Press. His second volume, containing 350,000 names proposed between 1801 and 1850, was completed in 1933, and published by the Trustees of the British Museum. During the progress of this work Sherborn contributed several small papers to the ' Annals and Magazine of Natural History ' on the dates of publication of some monographs which were issued in serial form. His aid to the study of systematic zoology was indeed great, and on the completion of his Index the University of Oxford conferred on him the honorary degree of D.Sc.

Sherborn also had a wide interest in geology, old English literature, and other antiquarian subjects. He took an active part in the researches of Dr. Arthur W. Rowe on the English Chalk, and in those of Mr. Upfield Green on certain rocks in western Cornwall. He collected coins and other objects of archaeological interest which he gave to the British Museum, the Fitzwilliam Museum, and other institutions. He arranged the correspondence and other papers accumulated by Sir Richard Owen, and revised the scientific part of the ' Life of Sir Richard Owen ', which was published by his grandson, the Rev. Richard Owen, in 1894. Sherborn also revised and edited the new edition of our Library Catalogue in 1896, but otherwise did not take part in the activities of the Linnean Society. He was, however, a good friend of many Fellows, who remember with appreciation his kindly help in the literature of systematic zoology.

ARTHUR SMITH WOODWARD.

With the death of HANS SPEMANN, which took place in 1941, Biology has lost a master of research who, by a combination of acute logical analysis and technical skill in experimentation, has made outstanding contributions to the study of the causation and determination of animal form.

Born in 1869, the son of a publisher, Spemann started in his father's firm before turning to an academic career in the course of which he worked successively in the Universities of Würzburg, Rostock, Berlin and Freiburg, from the Chair of Zoology in which latter University he retired in 1935.

His first researches were morphological and devoted to the development of the tympanic cavity and trabeculae cranii of Amphibia. It is an interesting fact that this group formed the material for his research all his life.

About the beginning of the century, Herbst put forward the concept of formative stimuli in development, and Spemann saw in the correlation of the lens with the eye-cup an opportunity of subjecting the concept to an experimental test. As a result of operations on amphibian embryos of different species, involving removal of the eye-cup, grafting it under the skin in different parts of the body, and grafting strange skin over the eye-cup *in situ*, Spemann established the fact that the eye-cup possesses the property of inducing the formation of a lens out of epidermis overlying it.

By means of other experiments, Spemann tested the power of different regions of the amphibian embryo to differentiate according to the place of origin or the place of grafting of the regions tested. He found that at an early stage presumptive eye-cup material might be made to develop into anything according to where it is grafted. Later on it will only develop into an eye-cup, wherever it is. By these experiments Spemann provided the classical examples of the phenomena of dependent-differentiation and self-differentiation.

Another line of investigation, involving constriction of blastulae wholly or partially into two by means of a loop of child's hair, led to the production of perfect twin embryos from a single egg, or of *duplicitas anterior*. It is characteristic of Spemann's experiments that they usually led on to others. In the case of these constrictions, it was soon apparent that the position of the dorsal lip of the blastopore relatively to the plane of the constriction has an important bearing on the results. Unless a part of the dorsal lip of the blastopore is present, no perfect embryo can develop. The special properties of this region were further shown by experiments in which the upper hemisphere of a blastula was cut off, rotated through any angle, and stuck back again, when it was found that the neural tube, notochord and other axial structures arose in line with the dorsal lip of the blastopore out of whatever material lay immediately above it.

The next step was to make grafts of portions of blastopore dorsal lips, when it was found that they induced the host tissues to differentiate into the axial structures of an embryo. Thus was discovered the organizing property of the dorsal lip of the blastopore, in virtue of which it has been given the name of ' organizer '.

The field was now open to experimentation on a wide basis. Had the organizer a regional differentiation so as to account for the induction of head-structures as apart from trunk or tail-structures ; was there a regional qualitative susceptibility to induction on the part of host tissues ; could organizers induce host tissues of different species ; would such host tissues differentiate into structures not possessed by the species of

the organizer : was there a possibility of analysing the property of the organizer into physico-chemical factors ?

Spemann and the school he had built up around him devoted themselves to all these questions and attacked them experimentally with uniformly profitable results.

Having got to know the normal structure of his material with complete thoroughness, and having developed a precise technique for exchanging the position of parts of the living embryo, all Spemann's experiments were rigorously controlled, and resulted in clear answers to simple questions whether A was or was not dependent on B.

It might be said that Spemann's contributions to Biology were restricted by the limits which he set to the material on which he worked, but such a criticism would be ill-judged. In the first place he never missed an opportunity of following up the implications of his results, into whatever fields they might lead. For instance, after interfering with the development of the ear vesicle in newts, he observed that the resulting animals showed abnormal postures and modes of locomotion, leading to a correlation of great importance between structure and behaviour. Again, in connexion with the laterality of ear vesicles and with the phenomenon of *situs inversus viscerum*, which he was able to produce experimentally, he was led to a profound analysis of the problem of mirror-image symmetry and asymmetry in general. Then again, one of the problems which absorbed him most as a result of the constriction experiments was the question of the production of two ' minds ' as well as of two heads or two complete embryos out of one egg.

Lastly, it must be pointed out that the general principles of dependent differentiation and organizer-action which Spemann investigated so thoroughly in Amphibia are applicable to the entire animal kingdom.

Spemann collected his results together in a volume which was translated into English and published in 1938, under the title of ' Embryonic development and induction '. He delivered the Croonian lecture before the Royal Society in 1927, was elected to Foreign Membership of the Linnean Society in 1924, and received a Nobel prize in 1935.

G. R. de Beer.

E. J. Wortley, C.M.G., O.B.E., F.L.S.—Edward Jocelyn Wortley died in Barbados on 27 April 1942. An illness a year previously had sent him on leave for some months. He returned to Trinidad early in the year, but a further setback compelled him to resign a few weeks later and he died shortly afterwards.

He had been a member of the Linnean Society for many years, but seldom had the opportunity of attending its functions as practically the whole of his career was spent abroad.

Born in Jamaica in 1884, he received his early education in that colony and entered the Colonial Service in 1902 as an Assistant Chemist in the Jamaica Agricultural Department. After holding several positions in that department he was appointed Director of Agriculture, Bermuda, in 1913. From there he was posted to Nyasaland in 1920 again as Director of Agriculture. Wortley always used to maintain that the ten years he spent in this East African Colony were among the happiest

he had spent, and he always looked back on his service there with pleasure. In 1930 he returned to the West Indies as Director of Agriculture, Trinidad and Tobago, and he continued to hold the post until he retired. Wortley arrived in Trinidad at a critical time. The agricultural industry throughout the West Indies passed through a very difficult period in the thirties, and there were additional complications in Trinidad. The cacao industry, so long the mainstay of the Island, had fallen on evil days after the boom years of the war period, and the planters were threatened with ruin by the appearance of the dreaded "Witch broom" disease. Under Wortley's direction various relief measures were attempted. That these measures were not altogether successful was due not to any lack of effort on his part, but rather to circumstances over which he had no control. A catastrophic fall in prices prevented the adoption of the preventative measures advocated. To alleviate matters attempts were made to introduce alternative crops. His efforts towards establishing an export trade in bananas met with partial success in the earlier years, whilst the founding of a promising citrus industry was in no small measure due to his enthusiasm and efforts.

It was as an administrator that his particular qualities had most scope. His belief of the need for agricultural research was always evident, and he was deeply interested in this aspect of the Imperial College of Tropical Agriculture, of which he was a Governor. He was a good friend of the College, and by his tact and common sense helped to ensure that excellent relations were maintained between the scientific workers at the College and his own staff in the Department.

He had a highly developed sense of humour and a merry wit, being quick at repartee. These gifts enabled him to get essential measures passed by the Legislative Council with the minimum of friction or delay. An outstanding characteristic was his friendliness—one simply could not be angry with him. He played a good game of bridge and of tennis, and socially was he in great request, as he was a raconteur of no mean order and possessed an inexhaustible fund of stories.

It was hoped that he would have lived in retirement for many years, and if he had there is no doubt that he would have enjoyed them. His sudden death at the comparatively early age of fifty-eight came as a great shock to all his friends, and our deepest sympathy is extended to his widow and his son. GEOFFREY EVANS.

The death of C. H. WRIGHT, on 21 June 1941, deprived the Society of its oldest botanical Associate and one of the two remaining Associates who were elected during the past century. Wright, who was elected in 1896, was a zealous supporter of the Society and a regular attendant at the Meetings until his retirement from official life in 1929, when he left Kew to live in Devon.

Charles Henry Wright was born at Oxford in June 1864, and was educated at New College School and later at the Herbarium and Laboratories of the Oxford Botanic Gardens. For a short time he was also Demonstrator in Botany. He came to Kew in 1884, and held his appointment in the Herbarium for 45 years, retiring on 31 August 1929. Wright's principal charge at Kew was the Monocotyledons, and he specialized on

the petaloid families of this group and the Palmae. He also had charge of the Pteridophyta and Bryophyta, and paid considerable attention to the former group. His published work, however, was mainly on the Monocotyledons. He also elaborated many families for the African 'Floras' prepared at Kew. The most important of these were the Solanaceae and Palmae, and (with J. G. Baker) the Boraginaceae and Proteaceae for the 'Flora of Tropical Africa', and the Solanaceae, Boraginaceae, Chenopodiaceae, Polygonaceae and Thymelaeaceae for the 'Flora Capensis'. In the Society's Journal he published (conjointly with I. H. Burkill) a paper on 'Some African Labiatae with alternate leaves', and one on 'The Flora of the Falkland Islands'.

Wright was noted for his attention to detail, and soon became an expert proof-reader, and comparatively early in his career Sir William Thiselton-Dyer entrusted him with the editing of the manuscripts and the reading of the proofs of the text of the above-mentioned 'Floras', a task inexpressibly tedious to most minds, which, however, Wright accomplished ably and with apparent relish.

Through his work on the 'Floras', and having had the responsibility of caring for a world collection of Monocotyledons, Ferns and Bryophytes, Wright must have had a wide knowledge and general view of all groups of plants except the Lower Cryptogams, a fact which may have accounted for his being elected an Associate of the Society at the very early age of 32.

At Kew he also was responsible for the very large collection of drawings and photographs in the Herbarium, and interested himself in various branches of routine work which were shunned by other members of the Staff. He was a lecturer to the Student Gardeners on Systematic Botany for 26 years and encouraged them to become acquainted with the Herbarium and Library.

He was much missed by the Staff when he retired under the age limit, on 31 August 1929, and went to live with his family at Seaton, where he continued to lead an active and useful life. Wright was of a very friendly disposition and made a point of welcoming and encouraging newcomers to the Herbarium.

A. D. Cotton.

BENEFACTIONS.

LIST *in accordance with Bye-Laws, Chap.* XVII. *Sect.* 1, *of all Donations of the amount or value of Twenty pounds and upwards, received during the past five years.*

1938

The late Mr. E. T. Browne : A portion of his scientific library.

Mr. Francis Druce : The expenses of the Society's 150th Anniversary Celebrations, £197 10*s*.

The Royal Society : Donation in aid of the publication of Dr. M. Carleton's paper, ' The biology of *Pontania proxima* Lep., the Bean Gall Sawfly of Willows ', and Mr. I. Mackenzie Lamb's paper, ' A review of the genus *Neuropogon* (Nees et Flot.) Nyl., with special reference to the Antarctic species ', £200.

1939

The Royal Society : Donation in aid of publications, £200.

The Percy Sladen Memorial Fund : Cost of printing and illustrating ' Transactions ', 3rd ser., vol. i, part 1.

1940

The late Major J. R. G. Gwatkin : An extensive collection of paintings of flowering plants, mainly British.

The Royal Society : Donation in aid of publications, £100.

The Percy Sladen Memorial Fund : Cost of printing and illustrating ' Transactions ', 3rd ser., vol. i, part 2.

1941

The late Mr. Francis Druce : (1) £200 for general purposes of the Society ; (2) a selection of books from his library, including some rare early botanical works.

Rockefeller Foundation : Donation in aid of publications, £100.

Carnegie Corporation of New York, $8,060, for the preparation of a photographic record of the collection and manuscripts of Carl Linnaeus.

The late Sir Arthur Evans : Portrait in oils of John Dionysius Ehret, F.R.S., by George James, A.R.A., 1767.

1942

Rockefeller Foundation : Donation in aid of publications, £200.

The Royal Society : Donation in aid of publications, £100.

India Office Library : Complete set of The Linnean Society of London's publications.

ADDITIONS AND DONATIONS

TO THE

LIBRARY

1941–2

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

The books here catalogued as bequeathed by the late Mr. Francis Druce cannot be consulted until after the war.

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[At end the printer's mark of Jehan Janot.] [FRANCIS DRUCE BEQUEST.]

Grete Herball. The grete herball / whiche geueth parfyt knowlege and under / standyng of all maner of herbes & there gracyous vertues, &c. [*Colophon,—*] (Printer's mark of Peter Treveris.) *Imprentyd at London in South= / warke by me Peter Treueris, dwel / lynge in the sygne of the wodows. / In the yere of our lorde god. M.D.xxvi. the xxvij day of July.*
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INDEX

Abrus, 170.
Acacia, 92, 97, 177.
Acanthomyops, 110.
Accounts, 190.
Achyranthes, 103.
Acorypha, 69.
Acraea, 13, 38.
Acrididae, revision of three genera, 69.
Actinosphaerium, 203.
Additions to Library, 302.
Adenanthera, 170.
Adventive flora of Fiji, 92.
Aeschna, 200.
Aeschynomene, 96.
African wild birds eating butterflies, 10.
Agathis, 156.
Ageratum, 99.
Agnia, 159.
Agrion, 198.
Agromyza, 102.
Agropyron, runners perforating various objects, 119.
Agrostis, 117, 176.
Ahnfeldtia, 241.
Alam, M., death, 1 ; obituary, 270.
Alaria, 247.
Albizzia, 98.
- - *Julibrissin*, longevity of seed, 183.
Aletis, 42.
Algeria, ecol. survey of some inland saline waters of, 120.
Alisma, 174.
Alona, 254, 255, 257.
Alonella, 257.
Alonopsis, 257.
Alternanthera, 103.
Alveolina, 121.
Alysicarpus, 96.
Amaranthus, 103, 173.
Amblystoma, 198.
Amauris, 13, 39.
Ammophila, 7.
Amoeba, 203.
Anachalcos, 36.
Anagallis arvensis, abnormal seedlings, 88.
Anchistropus, 258.
Andronymus, 42.
Anemone Pulsatilla, 9.
Angler fish, lure of, 197.
Anguilla, 163.
Anguis, preying, 209.
Anisomeles, 94.
Anniversary Meeting, 184.
Anoa, 140.
Anser, 202.
Antanartia, 13.
Antennaria, 117.
Ants, observations on the nest odours of, 109.
Apium, 94.
Aplopus, 196.
Aquilegia Einseleana f. *Schleicheri*, forma nova, 259.
Arber, A., on Nehemiah Grew's first marriage, 166.
Arcella, 258.
Arctostaphylos, 171.
Arenaria, 118.
Arenga, 67.
Argiopid spider, an American, in England, 46.
Arhopala, 159.
Arizelocichla, 4.
Artamus, 40.
Asclepias, 100.
Ascophyllum, 231, 239, 242, 244, 246, 249, 250, 252.
Aspidiscus, 233.
Associate, election of, 65, 86, 107 ; vacancies in list of, announced, 115.
Asterias, 262.
Asystasia, 102.
Atella, 13.
Atylosia, 97.
Auditors elected, 115.
Australian elements in Bornean flora, 155.

Babbler, food, of, 42.
Baeckea, 155.
Bangia, 235.
Banksia, 177.
Baoris, 42.
Barnes, B., appointed Deputy Treasurer, 1 ; member of Council, 194 ; Deputy Treasurer and Vice-President, 194 ; seedling abnormalities in *Anagallis arvensis*, 88 ; on potato pierced by *Agropyron*, 119 ; white flowers in *Ranunculus Flammula*, 58 ; observations of the Smoke fly, 115.
Baruah, H. K., election, 65, 86, 107.
Basella, 103.
Bauhinia, 97.
Beadle, L. C., an ecological survey of inland saline waters of Algeria, 120.
Belenois, 40.
Bell, J. H., election, 119, 166.
Bell, P. J., election, 119, 218.
Bellairs, d'A., on Jacobson's organ in snakes and lizards, 48.

Belonogaster, 205.
Belus, 159.
Benefactions, 301.
Betts, 198, 207.
Bhaduri, Param Nath, admitted, 106; election, 1, 46, 49.
Bibby, H. C., admitted, 184; election, 1, 46, 49.
Bidder, G. P., on evidence for Wegener's theory about the Atlantic, 164; on zonation of animals, 236.
Bifurcaria, 241.
Biogeography of the Indo-Australian Archipelago, 120.
Birds, seed-distribution by, 96, 98, 101, 102; selection of insects for food, 10.
Birds' Eggs, Salmon collection of, transferred to British Museum, 65.
Bixa, 94.
Blechum, 94.
Blister beetles, 42.
Boa, preying, 211.
Bocagea, 263.
Boerhaavia, 103.
Bombina, 197.
Bombyx, 214.
Boophilus, 211.
Borassus, 67.
Borreria, 99.
Botanical Secretary (I. H. Burkill) elected, 194.
Bosmina, 253, 254, 255, 256.
Botrychium, 117.
Bracher, R., death, 1; obituary, 270.
Brachyaria, 106.
Brachycerus, 36.
Brassica, 94, 168, 177.
—— *monensis*, 4.
Brett, M. A., appointed a scrutineer, 185.
Brooks, F. T., member of Council, 194.
Browne, The Lady Isabel M. P.; on the Caytoniales, 48.
Bryophyllum, 98.
Buccinum, 213.
Bucorax, 37.
Bufo, 197, 198.
Bugs, preying, 209.
Bulbul eating flowers, 96.
Bunodactis, 221.
Burkill, I. H., member of Council and Botanical Secretary, 194; on Committee for record of Linnaean collections, 187; on migrations of butterflies, 87; on the history of biogeographic divisions of the Indo-Australian Archipelago, 127; on John Ray, 10; a tuber of *Tamus* perforated by *Agropyron*, 119.
Burne, R. H., member of Council, 194; elected Auditor, 115.
Burton, E. St.J., election, 115, 119, 166.
Burton, W. G., election, 49, 65, 107; adm., 119.
Busk, Lady, obituary, 271.
Butler, F. B.-L., obituary, 271.
Butterflies, selection by birds as food, 10; migrations of, 86.
Byblia, 13, 42.
Bycanistes, 37.
Bythotrephes, 253.

Cacatua, 129.
Caesalpinia, 93, 97.
Cairina, 208.
Cajanus, 96.
Calliptamus, 69.
Callithamnion, 236.
Calman, W. T., on Whale marking, 116.
Caloptenopsis, 69.
Caloptenus, 69.
Calothrix, 236.
Campbell, M. S., as representing the Society on the Phenological Committee, of the Royal Meteorological Society, 186.
Campecopea, 233.
Camptocercus, 256.
Canavalia, 97.
Capsicum, 102.
Cardamine, 94.
Cardiospermum, 96.
Carex, 117.
Carnegie Corporation, grant from the, 186.
Carpenter, G. D. Hale, on African wild birds eating butterflies, 10.
Carter, G. S., member of Council and Vice-President, 194.
Caryota, 67.
Cassia, 94, 97, 101, 170.
Cassytha, 103.
Casuarina, 151, 155, 156, 177.
Catacroptera, 13.
Catopsilia, 13.
Caulerpa, 236.
Caytoniales, their position (Harris), 47.
Celerio as migrant, 86.
Centaurea, 93.
Centropus, 14.
Centropyxis, 258.
Ceratophyllum, 104.
Cervus, 141.
Chaetangium, 222.
Chamaerops, 67.
Chapman, V. J., zonation of Marine Algae on the sea-shore, 239.

Charaxes, 13, 45.
Chatterjee, D., revision of the Indian and Burmese species of *Sageraea*, 263.
Chear, J., election, 1, 46, 49; adm., 106; on natural history films, 108.
Chenopodium Vulvaria, 9.
Chick, film of, shown, 107.
Chicks, newly hatched, behaviour of, 204.
Chlorophoneus, 14.
Chondrus, 247.
Choreocolax, 236.
Chrysopogon, 106.
Chthamalus, 233.
Chydorus, 255, 258.
Cichlasoma, 206.
Cisticola, 14.
Citrus, 177.
Cladophora, 244.
Clathrina, 236.
Cleome, 94.
Clerodendron, 102.
Clidemia, 98.
Climate of the Indo-Australian Archipelago, 124.
Clitorea, 96.
Cocos, 68.
Coleus, 103.
Colman, J., Intertidal enigmas, 232.
Commelina, 104.
Commersonia, 92.
Competition and zonation, 225.
Coracina, 14.
Corbet, A. S., considerations based on the Rhopalocerous fauna (Discussion on Wallace and Weber lines), 143.
Corchorus, 95.
Coriandrum, 99.
Cornus, 176.
Corstorphine, R. H., death, 184; obituary, 272.
Corvus, 207.
Cosmos, 100.
Cotoneaster, 170.
Crataegus, 171.
Crataeva, 94.
Crateropus, 37.
Crenis, 13.
Crepis, 94.
Crotalaria, 96.
Cryptarus, 208.
Cucurbita, 174, 176.
Cuphea, 98.
Cuscuta, 101.
Cycas, 92.
Cyclopterus, 197.
Cyperus, 105.
Cypria, 258.

Dacrydium, 155, 156.
Danaida, 38.
Danais as migrant, 86.
Danaus, 13.
Dandy, J. E., member of Council, 194; on Committee for record of Linnaean collections, 187.
Danthonia, 117.
Daphnia, 253, 254, 256.
Datura, 101.
Deaths recorded, 185.
Deer and objects in motion, 201.
Delesseria, 236.
Delf, E. M., member of Council, 194; on the Caytoniales, 48; on veldt spiders, 47; significance of the exposure factor in relation to zonation, 234.
Delphinium, 177.
Deputy Treasurer (B. Barnes), appointed, 1.
Desiccation and zonation, 222.
Desmanthus, 93.
Desmodium, 96.
Dicrurus, 14.
Difflugia, 203, 258.
Digitalis purpurea campanulata (monstrosa), 57.
Digitaria, 173.
Dipterocarpaceae as a character in the Indo-Australian Archipelago, 135, 151.
Discussion on Wallace and Weber lines, 120.
Distribution of life, factors affecting the (Scrivenor), 120; of organisms between tidemarks in South Africa, 219.
Dolichos, 96.
Dollman, J. G., death, 119; obituary, 273.
Drift-wood for transporting animals, 139.
Drimys, 155.
Druce, Francis, bequest, 189, 302.
Dryoscopus, 39.
Ducklings, instinctive fear in, 207.
Dumontia, 247.
Duncan, F. M., on the photographic record of the Linnaean Collections, 56.
Dung beetles, instinctive behaviour, 211.
Durvillea, 236.
Dytiscus, 200.

Echinocystis, 170.
Ehret, gift of portrait of, 189.
Eichhornia, 104.
Elections reported, 185.
Eleocharis, 105.
Elephantopus, 99.

Eleutheranthera, 100.
Emilia, 100.
Emmenanthe, 182.
Enteromorpha, 236, 240, 244.
Entomostraca of the bottom deposits of Windermere, 253.
Epeira, 204.
Epicotyl, dormancy of, 171.
Erechthites, 100.
Erica, 177.
Erigeron, 99.
Eronia, 13.
Eryngium, 94.
Eucalyptus, 151.
Euglypha, 258.
Eugryllacris, 158.
Eulalia, 92.
Euphorbia, 103, 104.
Euploea, distribution in the Indo-Australian Archipelago, 146.
Eurycercus, 255, 256.
Eurycus, 159.
Eurytela, 13.
Euthalia, 147.
Evans, Sir Arthur, bequest of a portrait, 189.
Evans, Sir Geoffrey, on an American spider in Britain, 47.
Experiments on African wild birds eating butterflies, 10.

Fellows deceased, withdrawn, removed, 185.
Fern, film of, shown, 107.
Fiji, adventive and weed flora of, 92.
Films, biological, shown, 107.
Fimbristylis, 105.
Fish, freshwater, distribution of, in the Indo-Australian archipelago, 163.
Fisher, J. M. McC., election, 217, 218.
Flint, E. A., election, 86, 107, 166; admitted, 184.
Flintoff, R. J., death, 1; bequest, 189; obituary, 275.
Flippance, F., death (wrongly) reported, 119.
Flora of Fiji, 92.
Flora of SW. Greenland, 117.
Flynn, T. T., and Hill, J. P., the later stages of cleavage and the formation of the primary germ layers in the Monotremata, 68.
Foeniculum, 99.
Formica, 110.
Fossil palm wood, 65.
Francolinus, 36.
Franklyn, C. A. H., election, 217, 218.
Fraser, F. C., member of Council, 194; on Mesorostral ossification in *Ziphius cavirostris*, 50.
Fraxinus, 175.
Fucus, 230, 231, 232, 235, 236, 239, 242, 244, 247, 249, 250, 252.

Gadus, 197.
Gammarus, 214.
Gardiner, A. C., member of Council, 194.
Gasterosteus, 198.
Gazelle, and objects in motion, 201.
Gebiet as a term in Biogeography, 128.
Gegenes, 13.
Gelidium, 226, 241.
Gentiana, 117.
Geology of the Indo-Australian Archipelago, 120.
Geotrupes, 211.
Geranium sanguineum, 9.
Germination of seeds, literature-list, 179.
Gigartina, 222, 235, 247.
Glossosiphonia, 203.
Gordon, I., elected Auditor, 115.
Graptoleberis, 257.
Greenland, SW., Flora and Phytogeography (Polunin), 117.
Greenwood, William, on the adventive and weed flora of Fiji, 92.
Grevillea, 182.
Grew, Nehemiah, a biographical note, 166.
Griffiths, B. M., death, 119; obituary, 278.
Grove, A., death, 86; obituary, 278.
Grundy, Sir Cuthbert C., a fasciated *Ranunculus bulbosus* (exhibit), 217.
Gryllacris, 158.
Gynandropsis, 94.

Haematopinus, 212.
Hakea, 177.
Halcyon, 36.
Halesia, 171.
Halidrys, 241.
Hall, Patrick M., death, 1; obituary, 280.
Halophila, 104.
Hamanumida, 13.
Hamm, A. H., exhibit of a Digitalis, 49.
Harris, T. M., member of Council, 194; the position of the Caytoniales, 47.
Hay, T., on curious behaviour of some seeds in germination, 182.
Hedyotis, 99.
Heleopera, 258.
Helianthus, 177.
Helleborus, 183.
Hemichromis, 206.

Hemiclepsis, 203.
Henotesis, 13.
Hentschel, C. C., member of Council, 194.
Herpobdella, 203.
Hesperia, 13.
Hevea, 178.
Hibbertia, 92.
Hibiscus, 95.
Hierochloe, 117.
Hill, Sir Arthur W., *Streptocarpus nobilis*, with cleistogamic flowers, 1; death, 46; obituary, 280.
Hill, J. P., *see* Flynn, T. T.
Hipocrita, 213.
Hirudo, preying, 209.
Hirundo, 44.
Hooper, C. H., on migrations of butterflies, 87.
Hoopoos, food of, 43.
Hubbard, C. E., on the perforating power of *Agropyron* runners, 120.
Hyalosphenia, 258.
Hydrocotyle, 99.
Hypnea, 222.
Hypolimnas, 13.

Ice Age, effect on sea-level in Indo-Australasian archipelago, 153.
Idotea, 197, 201.
Impatiens, 171.
Imperata, 105.
Indigofera, 97.
Indo-Australian Archipelago, biogeographic division of, 120, 127.
Indo-Malayan elements in Australia, 156.
Inland saline waters of Algeria, ecol. survey, 120.
Insect-distribution in Indo-Australian archipelago, 157.
Insects, selection by birds as food, 10.
Instinctive behaviour, perceptual and sensory signs of, 195.
Insurance (War Damage), 189.
Intertidal enigmas (Colman), 232, 238.
Introduction of weeds to Fiji, 92.
Ipomoea, 101.
Irrisor, 38.
Ischaemum, 105.
Isotoma, 94.
Ispidina, 14.
Ixodes, preying, 211.

Jackdaw, instinctive fear in, 207.
Jacobson's organ in snakes and lizards, 48.
Jatropha, 104.
Johnson, J. W. H., death, 119; obituary, 285.
Juncus, 117, 152.
Jussiaea, 98.

Kaul, K. N., anatomy of the stem of palms and the problem of the artificial genus *Palmoxylon*, 65; method of preparing large sections of plants by grinding [Title only], 218; a way of taking up the nest odour of ants, 113.
Kerr, A. F. G., obituary, 285.
Krakatau, re-stocking of, 140.
Kripa, 69.
Kyllinga, 105.

Lacey, W. S., election, 1, 46, 49.
Ladybirds, 43.
Laminaria, 233, 236, 247.
Laniarius, 14.
Lanius, 195, 204.
Lantana, 102; insect enemies of, 102.
Larnaca, 158.
Lasaea, 233.
Lathyrus, 170, 182.
Latitudinal belts in Indo-Australian archipelago, 125, 162.
Laurencia, 236, 247.
Lemna, 104.
Leptodora, 253, 258.
Leptosia, 13.
Leptospermum, 155, 177.
Leptothorax, 110.
Lesquereusia, 258.
Lesser Sunda islands, biogeography of, 134, 162.
Lettuce, 169.
Leucas, 103.
Leuceronia, 40.
Leydigia, 255.
Librarian and Assistant Secretary's report, 185.
Library, additions to, 302; report on, 185, 186.
Lice, preying, 209.
Lichina pygmaea, population of, 233.
Lilium, 172, 177.
Limnanthemum, 100.
Linnaean collections, report on, 185; a photographic record of, 50, 186.
Linnean medal, award suspended, 189.
Liogryllus, 206.
Liothrips, 98.
Liparis Loeselii, 9.
List of the Society, report on, 185.
Lithothamnion, 223, 232.
Littorina, 227, 229, 232, 237.
Lizards, Jacobson's organ in, 48.

Lobelia, 94.
Lochnera, 100.
Lodoicea, 182.
Lophius, 197.
Lophoceros, 38.
Lourea, 96.
Lucilia, 211.
Lycaenids, distribution of genera in the Indo-Australian Archipelago, 144.
Lyperosia, 210.
Lythrum, 173.

Maba, 42.
Macaca, 140.
Mackintosh, N. A., member of Council, 194; distribution of the Whalebone Whales in the Southern Ocean, 116.
Macrocystis, 236.
Magnolia, 184.
Maize, film of, shown, 107.
Malvastrum, 95.
Man as a character in the biogeography of the Indo-Australian archipelago, 141.
Marine Algae, zonation, 239.
Mariscus, 105.
Meibomia, 93.
Melaleuca, 135, 155, 156.
Melanitis, 13.
Melastoma, 98.
Melilotus, 170.
Melobasis, 159.
Melville, R., member of Council, 194.
Merops, 14; selection of insects taken for food, 17.
Metcalfe, C. R., on the anatomy of the stems of palms, 68.
Metromerus, 83; revision of genus, 69.
—— spp., 83.
Michelia, 184.
Microsania, observations on, 115.
Migration of Butterflies, 86.
Mikania, 100.
Millipede, 42.
Mimosa, 98.
Mimulus, 173.
Mirabilis, 103.
Miranda, 47.
Miscanthus, 92.
Monotremata, cleavage and primary germ layers in the, 68.
Momordica, 99.
Monro, C. C. A., death, 218; obituary, 286.
Montane and lowland floras in Indo-Australia, possible diverse origin, 148.
Montane plants invading the Indo-Australian Archipelago, 136.
Moon, phases of, and germination of seeds, 178.
Montia, 117.
Morley, B. D. W., election, 1, 46, 49: adm., 106; observations on the nest odours of ants, 109.
Mosquitoes, preying, 209, 210.
'Mossy forest' in Borneo, 155.
Movement of prey and capture, 195.
Mucuna, 97.
Mulberry, 168.
Mycalesis, 13, 40.
Mycorrhiza, 177.
Mylothris, 13.
Myrmelion, 205.
Myrmica, 110.
Mytilus, 221, 225, 226, 228.

Nassa, 214.
Nature-Preservation in Post-War Reconstruction, 49, 115.
Nebela, 258.
Nelumbium Nelumbo, longevity of seed, 174, 183.
Nemesis, 182.
Nemophila, 173.
Neptis, 13, 40.
Nest odours of Ants (Morley), 109.
Newman, C. A., death, 1; obituary, 289.
Nicotiana, 171, 173.
Nicsara, 159.
Nigella, 173.
Norman, J. R., member of Council, 194; on a photographic record of the Linnaean collections, 50; on Committee for record of Linnaean collections, 187; on the distribution of freshwater fish in the Indo-Australian archipelago, 163.
Nothofagus, 184.
Nummulites, 121.

Obituary Notices, 270.
Ocimum, 102, 103.
Octomeris, 225, 226, 227, 228.
Ocypoda, 200.
Oenothera, 167.
Officers elected, 194.
Olapa, 42.
Oldenlandia, 99.
Oldham, C., death, 119; obituary, 291.
Osborn, T. G. B., member of Council, 194.
Osprynchotus, 43.
Ostrea, 222.
Oxalis, 95; explosive capsule of, 95.
Oxystele, 229.

Pachyrrhizus, 92.
Padraona, 13.
Palmocarpon, 66.

Palmophyllum, 66.
Palmoxylon, an artificial genus, 65.
Palms, anatomy of the stem of, 65.
Panicum, 106, 173.
Papilio, 13.
Parasitus, 116.
Parnara, 13.
Passiflora, 94, 98, 99.
Patella, 225, 227, 228.
Paulinella, 258.
Pecten, 202, 214.
Pediculus, preying, 210.
Pelvetia, 231, 232, 235, 239, 242, 249, 250.
Peracantha, 258.
Phacelia, 173.
Phalangers, 140, 159.
Phaseolus, 96, 178.
Philanthus, 198.
Phoenix, 67.
Phomopsis, 177.
Phyllanthus, 104.
Phyllastrephus, 37.
Phyllocladus, 155.
Physalis, 102.
Pieris, 13, 196, 213; as migrant, 86.
Pinus, 169.
Pipilo, 207.
Pirata, 204.
Pisaura, 200.
Piscicola, 203.
Pithecellobium, 97, 170.
Planema, 13.
Platylesches, 13.
Plectranthus, 103.
Plocamium, 234.
Plumbago, 100.
Poa, 117, 118, 176.
Pogonocichla, 14.
Polistes, 205.
Pollination of *Clerodendron* by birds, 102.
Polunin, N., on the Flora of SW. Greenland, 117; on Whales, 116.
Polygala, 94.
Polysiphonia, 236.
Polystomella, 203.
Pomatoleios, 226.
Populus, 167.
Portulaca, 94.
Posidonia, 211.
Postelsia, 240.
Potamogeton, 117.
Potato, seeds, 174.
Precis, 13.
President (Dr. E. S. Russell, lected, 194; Presidential Address (Perceptual and sensory signs in instinctive behaviour), 195; on the welfare of the Society, 185; on the photographic record of the Linnaean Collections, 56.
Primocarex, 151.
Primula, 174, 183.
Priophorus, 213.
Prosopogryllacris, 158.
Province as a term in Biogeography, 128.
Pseudacraea, 13.
Psidium, 98.
Pueraria, 92.
Pycnonotus, 14.
Pycraft, W. P., death, 184; obituary, 293.
Pycreus, 105.
Pyrameis, 13.
Pyramids, change of axis, 164.
Pyrola, 176.
Pyronema, 116.
Pyrus, 171.
Pyura, 225, 226.

Quadrula, 258.
Quercus, 175.

Raffill, C. P., on difficulties in germinating seeds, 184.
Rain-forests, location of, in Borneo, 154.
Raisin, C. A., donation, 217.
Ramsbottom, J., member of Council, 194; Chairman of Committee for record of Linnaean collections, 187; on the germination of old seeds, 183; on John Ray, 10.
Rana, 197, 198, 202.
Ranatra, 204.
Ranunculus, 152.
—— *bulbosus*, fasciation in, 217.
—— *Flammula*, white flowers in, 58.
Raven, C. E., election, 65, 86, 107; adm., 118; new light on John Ray, 3.
Realm as a term in Biogeography, 127.
Region as a term in Biogeography, 127.
Reid, D. M., member of Council and Vice-President, 194; elected Auditor, 115; on the value of biological films, 108.
Removal from the Society, 185.
Rhapis, 67.
Rhea, 208.
Rhipicephalus, 211.
Rhizoclonium, 236.
Rhizopalmoxylon, 66.
Rhodnius, 209.
Rhododendron, 177.
Rhodymenia, 234.
Rhopalocampta, 13.
Rhopalocera as characteristics in the biogeography of the Indo-Australian Archipelago, 143.

Rhynchotalona, 257.
Richards, P. W., ecological segregation in Indo-Australian Archipelago, 154.
Ricinus, 104.
Riddelsdell, H. J., death, 1; obituary, 294.
Rivina, 103.
Robins, E. A., on an American spider in England, 40.
Robinson, G. W., on conditions for germinating seeds, 182.
Romneya, 182.
Ropalidia, 205.
Rosaceous seeds, after-ripening of, 170.
Ross-Craig, S., election, 49, 65, 107; admitted, 119.
Ruellia, 102.
Rumex, 167.
Ruppia, 104.
Russell, E. S., member of Council and President, 194.

Sager, J. L., death, 115, 119.
Sageraea, revision of Indian and Burmese species, 263.
Salamander, 197.
Salamis, 13.
Salisbury, A. E., services in the making of a record of the Linnaean collections, 187.
Salmon coll. of Birds' Eggs transferred to Brit. Mus. (N. H.), 65, 188.
Samanea, 97.
Sandwith, N.Y., appointed a scrutineer, 185.
Sarangesa, 13.
Savage, S., on Committee for record of Linnaean collections, 187; on a catalogue of the Linnaean Herbarium, 56; on John Ray, 10.
Saxicola, 14.
Scaevola, 155.
Scarabaeus, 211.
Schima, 135.
Scourfield, D. J., appointed a scrutineer, 185; Entomostraca of the bottom deposits of Windermere, 253.
Scrivenor, J. B., geological and climatic factors affecting the distrib. of life, 120; on Wegener's theory, 163.
Scrutineers appointed, 185.
Secretaries elected, 194.
Sealy, Mrs. R. J., elected, 107.
Sectional Committees, formation of, 166, 186.
Sections of large fossil plants, method of preparing, 218.
Seedling abnormalities in *Anagallis arvensis*, 88.
Seeds, after-ripening of, 170; germination of, 167; longevity of, 167, 183; vegetable, deterioration of, 168.
Selenia, 196.
Senebiera, 93.
Senecio, 152.
Sesamum, 102, 170, 177.
Sesbania, 93, 97.
Seseli Libanotis, 9.
Sesuvium, 99.
Setaria, 173.
Shaw, H. K. Airy, divisions of Indo-Australian archipelago from the botanical standpoint, 148.
Sheldon, J. J., death, 86; obituary, 295.
Sherborn, C. D., death, 218; obituary, 295.
Shove, R. F., suggestions regarding biological films, 108.
Shrikes, dealing with prey, 195.
Sida, 95.
Silene, 167.
Sinopithecus, 140.
Sisyrinchium, 183.
Skalińska, M., *Aquilegia Einseleana* f. *Schleicheri*, forma nova, 259.
Smith, Malcolm A., member of Council and Zoological Secretary, 194; on Committee for record of Linnaean collections, 187; on migration of butterflies, 87; divisions of Indo-Australian archipelago as indicated by the vertebrata, 138.
Smoke fly, observations on, 115.
Snakes, Jacobson's organ in, 48.
Sclanum, 101.
Sonchus, 100.
Sorghum, 106.
South Africa, intertidal zonation in, 219.
Southern Ocean, distrib. of Whalebone Whales in, 116.
Spathoglottis, 92.
Spemann, H., obituary, 295.
Sphingomorpha, 40.
Sphodromerus, 70.
—— *arab*, sp. n., 75.
—— *calliptamoides*, sp. n., 79.
—— *luteipes rubripes*, subsp. n., 82.
—— *rathjensi montanus*, subsp. n., 81.
—— *somali*, sp. n., 81.
—— *tuareg*, sp. n., 78.
—— *undulatus salinus*, subsp. n., 82.
—— —— *pedestris*, subsp. n., 82.
—— spp., 71-83.
Sphodronotus, gen. n., 70, 84; *cf.* 84.
—— *cyclopterus*, sp. n., 84.
Spider of the family Argiopidæ, occurrence in Hampshire, 46

Spiders, preying, 200, 204.
Sponges and intertidal zonation, 236.
Sporobolus, 173.
Stachytarpheta, 101, 102.
Staff, pensions of, 189.
Stanbury, F. A., election, 1, 46, 49.
Starlings, instinctive fear in, 208.
Stephenson, T. A., causes of the vertical and horizontal distrib. of organisms between tidemarks in South Africa, 219; replies, 238.
Stern, F. C., member of Council and Treasurer, 194; his work as Treasurer to be done by a Deputy, 1.
Stomoxys, 210.
Streptocarpus nobilis, cleistogamy of, 1.
Striga, 173.
Strongylognathus, 111.
Stylotella, 236.
Styphelia, 155.
Submergence and zonation, 229.
Subscriptions, remissions during service with armed forces, 186.
Sugar beet, seeds, 176.
Sunda and Sahul shelves, 122, 139, 150, 160.
Suriana, 95.
Svenska Linné-Sällskapet, congratulations to, 165.
Swynnerton, C. F. M., on African wild birds eating butterflies, 10.
Symphoricarpus, 171.
Symposium on intertidal zonation, 219.
Synedrella, 100, 101.

Tams, W. H. T., election as Associate, 65, 86, 107; on Committee for record of Linnaean collections, 187.
Tamus, 171; tuber perforated by *Agropyron*, 119.
Tanaecia, distribution of species in the Indo-Australian Archipelago, 145.
Taxus, 171.
Tchitrea, 14.
Tea seed, 178.
Telephonus, 35.
Temperature and zonation, 224.
Tenison, W. P. C., election, 65, 86, 107; adm., 115.
Tephrosia, 97.
Terias, 13.
Termites, 42.
Tetramorium, 111.
Thais, 227.
Thecla, 102.
Thomas, Hamshaw, message from, 48.
Thunbergia, 102.
Tilapia, 206.
Tilia, 171, 174.
Tincker, M. A. H., on germination of seeds, 167.
Tithonia, 100.
Trapa, 174.
Treasurer (F. C. Stern) elected, 194; Deputy appointed, 1.
Treasurer's annual report, 184; accounts, 190.
Tridax, 100.
Trinema, 258.
Tristania, 155, 156.
Triumfetta, 95.
Turdus, 205.
Typha, 169, 174.

Ulva, 240, 247.
Urena, 95.
Uvarov, B. P., revision of the genera *Sphodromerus*, *Metromerus* and *Sphodronotus*, 69; on biogeographic divisions, 165.

Vandellia, 102.
Vanessa as migrant, 86.
Verbascum, 167.
Verbena, 94.
Vernonia, 99.
Veronica spicata, 9.
Vertebrata, divisions of Indo-Australian archipelago as indicated by the, 138.
Viability of seeds, determination of, 178.
Vicia, 170.
Victoria, 183.
Vigna, 97.
Vipers taking prey, 197.

Wakefield, E. M., elected Auditor, 115.
Wallace line, 120.
Wallacea as a term in Biogeography of the Indo-Australian Archipelago, 135, 142.
Waltheria, 95.
Warm-blooded animals and biogeographic boundaries, 133.
Water, movement of, and *Buccinum*, 213.
Watt, M., *Digitalis purpurea campanulata* (monstrosa), 57.
Wave-action and zonation, 225.
Weber line, 120.
Weed flora of Fiji, 92.
Wegener's theory and earth-movements in Indo-Australian archipelago, 123, 153, 159.
Weinmannia, 155.
Weiss, F. E., on the Caytoniales, 48; on abnormal seedlings of *Anagallis*, 88.

Welfare of the Society, report on, 185.
Williams, C. B., migration of Butterflies, 86.
Willughby, Francis, as zoologist, 8.
Wilmott, A. J., on natural history films, 108; on the nest odours of ants, 113; on Committee for record of Linnaean collections, 187.
Withdrawals from Fellowship, 185.
Whales, Whalebone, distrib. in the Southern Ocean, 116.
Wheeler, L. R., on bird-preferences for insects, 45; on migrations of butterflies, 87.
Windermere, bottom deposits, 253.
Woolfe, H. B., on natural history films, 107.
Wortley, E. J., obituary, 298.
Wright, C. H., obituary, 299.

Xanthium, 99, 174.
Xiphophora, 236.

Ypthima, 13.

Zamenis, 197.
Zeuner, F. E., insect distribution in Indo-Australian archipelago, 157; on evidence for Wegener's theory, 164.
Ziphius, Mesorostral ossification in, 50.
Zizyphus, 95.
Zonation, exposure factor in, 234; intertidal, symposium on, 219; of Marine Algae, 239.
Zoological Secretary (Malcolm A. Smith) elected, 194.
Zoological Society joins in meetings, 49, 186.

[*Part 3, pp. 217–315, published 17 June 1943.*]

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CONTENTS

	Page
List of Publications issued	iv
Proceedings of the 154th Session	1
Treasurer's Accounts	190
Presidential Address	195
Obituaries	270
Benefactions, 1938–1942	301
Additions and Donations to Library	302
Index	306

PURLICATIONS : From June 1941–May 1942

Proceedings, 153rd Session (1940–41) ; Parts 1 & 2.

CONTENTS (*continued*).

Page

A revision of the Indian and Burmese species of Sageraea (Annonaceae). By D. CHATTERJEE 263

Obituaries 270

Benefactions 301

Additions and Donations to the Library 302

Index 306

Title-page and Contents.